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# Unravelling the moons: review of the genera *Paratetilla* and *Cinachyrella* in the Indo-Pacific (Demospongiae, Tetractinellida, Tetillidae)

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## Abstract

*Paratetilla bacca* (Selenka, 1867) and *Cinachyrella australiensis* (Carter, 1886) occur in a broad range of marine environments and are allegedly widely distributed species in the Indo-Pacific. We coin the term 'moon sponges' for these species as they are spherical in shape with numerous porocalices resembling the lunar surface. Both species have a complex taxonomic history with high synonymization, in particular by Burton (1934, 1959). An examination of the junior synonyms proposed by Burton (1934, 1959) was conducted to establish the validity of the names. More than 230 specimens from Naturalis Biodiversity Center were reviewed that belong to the genera *Paratetilla* and *Cinachyrella* from marine lakes, coral reefs, and mangroves in Indonesia. The aim of the current study was to untangle the taxonomic history, describe the collection of moon sponges from Indonesia, and develop a key. We extensively reviewed the taxonomic literature as well as holotypes of most of the species synonymized by Burton. The taxonomic history of

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*Paratetilla* spp. and *Cinachyrella australiensis* showed some cases of misinterpreted synonyms, misidentifications, and lack of detailed descriptions for some species. The conclusion of the revision is that there are three valid species of *Paratetilla* (*P. arcifera*, *P. bacca*, and *P. corrugata*) and four valid species of *Cinachyrella* (*C. australiensis*, *C. porosa*, *C. paterifera*, and *C. schulzei*) in Indonesia. This is furthermore corroborated by molecular work from previous studies. *Paratetilla arcifera* Wilson 1925 and *C. porosa* (Lendenfeld, 1888) are resurrected. A full review of taxonomic history is provided as well as a key for identification of moon sponges from Indonesia. All species are sympatric and we expect that there are undescribed species remaining within the Tetillidae from the Indo-Pacific. Our current review provides the framework from which to describe new species in the genera *Paratetilla* and *Cinachyrella* from the Indo-Pacific.

**Keywords**

anchialine systems, coral reef, mangrove, marine lake, Porifera

## Introduction

Moon sponges include two good examples of allegedly widely distributed species in the Indo-Pacific: *Paratetilla bacca* (Selenka, 1867) and *Cinachyrella australiensis* (Carter, 1886). They are conspicuous dwellers of a broad range of marine environments, including coral reefs, rocky shores, and coastal mangroves, as well as landlocked marine systems called marine lakes (e.g. Hooper et al. 2000, de Voogd and Cleary 2008, de Voogd et al. 2009, Becking et al. 2011). We use the term 'moon sponges' as these species are spherical in shape with numerous porocalices resembling the lunar surface and colored various shades of yellow, orange and brown. This common name has now been adopted by different authors (e.g., Szitenberg et al. 2013). Naturalis Biodiversity Center houses hundreds of moon sponges with a great diversity in morphology that were collected in Indonesia from 2006–2011 with the aim to survey the sponge biodiversity.

The genera *Paratetilla* and *Cinachyrella*, belong to the family Tetillidae, suborder Spirophorina, order Tetractinellida, class Demospongiae. As spirophorids, they are characterized by the presence of rugose sigmaspires (van Soest and Hooper 2002). Similar to most tetillids, their globular shape is composed of triaenes and oxeas arranged in a radiate skeleton. Recent revisions of the order and the family have been compiled in the Systema Porifera by van Soest and Hooper (2002) and van Soest and Rützler (2002), respectively. Although 26 nominal genera have been described, only ten valid genera are recognized, which are differentiated by the presence of cortical structures, specialized pore-sieves (porocalices) and composition of the complementary spicules (Rützler 1987, van Soest and Rützler 2002, Carella et al. 2016) (Table 1). The principal types of spicules of this family are: 1. *Megascleres*, oxeas and triaenes (pro-, plagio, ortho, and anatriaenes), and 2. *Microscleres*, microxeas and sigmaspires. Identification at species level is mainly based on the geometry and size range of all spicule types and presence/absence of triaenes (van Soest 1977, Rützler 1987, Rützler and Smith 1992, Lazoski et al. 1999, de Voogd and van Soest 2007, Carella et al. 2016).

The species *P. bacca* and *C. australiensis* share an obscure taxonomic history, including incomplete descriptions, intermingled identifications, and tens of different species synonymized (see synonyms of *C. australiensis* in Burton 1934: 523, and *P. bacca* in Burton 1959: 200). Therefore, we expected that a detailed revision would reveal species lumped together under both taxonomic entities. The aims of this paper are two-fold: (1) to review the taxonomic history of the genus *Paratetilla* and the species *Cinachyrella australiensis*, and (2) to identify and describe the different *Paratetilla* and *Cinachyrella* species from Indonesia in the Naturalis Biodiversity Center collection.

## Materials and methods

### Taxonomic revision

Literature from 1867 to date was reviewed in order to compile the descriptions of the 11 nominal species for the genus *Paratetilla* Dendy, 1905. The *Cinachyrella* species revision was based on the literature cited by Burton (1934), who lumped together 16 nominal species as synonyms of *Cinachyrella australiensis* (Carter, 1886). The World Porifera Database WPD (van Soest et al. 2018) was used as a valuable guide for consulting the valid species and addressing the literature review. Type material and reference collections deposited at the American Natural History Museum (**AMNH**) in New York, at the Smithsonian Institution National Museum of Natural History (**NMNH**) in Washington D.C., the Natural History Museum (**NHMUK**, formerly **BMNH**) in London, and the Naturalis Biodiversity Center in Leiden (**RMNH**), were examined. The majority of the holotypes were studied for the current research; the ones we did not review were either unavailable or the description of the text was clear and comprehensive.

### Sampling

Individuals of *Cinachyrella* spp. and *Paratetilla* spp. were collected by snorkelling and SCUBA diving during expeditions to Bali (2003), Bunaken (Sulawesi, 2006), Pulau Seribu (Java, 2005), Raja Ampat (Papua, 2007), Berau (East Kalimantan, 2008), and Ternate (Moluccas, 2009). Sampling was systematically achieved in marine habitats such as coral reefs and mangroves, and within marine lakes (Raja Ampat and Berau). Specimens were photographed *in situ* and notes made on morphological and ecological features such as color, size, depth, and substrate. A total of 237 specimens were collected and preserved in ethanol 70%; an additional 11 specimens from the Naturalis Biodiversity Center collection from Indonesia and elsewhere were reviewed as well as 20 type specimens. Table 2 provides an overview of sample numbers per species and Suppl. material 1 (Table S1) provides full collection details per sample.

**Table 1.** Valid genera of Tetillidae Sollas, 1888 and principal characteristics used to distinguish them. (+) present, (-) absent. (AN) Antarctic, (AT) Atlantic, (CA) Caribbean, (IP) Indo-Pacific. Modified from Rützler (1987), van Soest and Rützler (2002), Carella et al. (2016). Number of valid species consulted at the World Porifera Database (van Soest et al. 2018; accessed 04 Jun 2018).

| Genus | Cortex (reinforced by) | Porocalices (shape) | Accessory spicules | Valid species | Distribution |
|---|---|---|---|---|---|
| *Tetilla* Schmidt, 1868 | – | – | – | 54 | AT, CA, IP |
| *Craniella* Schmidt, 1870 | + (minute smooth oxea) | – | – | 42 | AN, AT, CA, IP |
| *Cinachyra* Sollas, 1886 | + (minute smooth oxea) | + (flask) | – | 3 | AN, AT |
| *Paratetilla* Dendy, 1905 | – | + (hemi-spherical or narrow) | + (calthrop-like) | 5 | IP |
| *Cinachyrella* Wilson, 1925 | – | + (hemi-spherical) | – | 42 | AT, CA, IP |
| *Amphitethya* Lendenfeld, 1907 | + (amphiclads) | – | + (amphiclads) | 2 | IP |
| *Fangophilina* Schmidt, 1880 | – | + (differentiated, narrow) | – | 4 | AT, CA, IP |
| *Acanthotetilla* Burton, 1959 | + (megacanthoxea) | + (narrow) | + (megacanthoxea) | 7 | AT, CA, IP |
| *Antarctotetilla* Carella et al., 2016 | pseudocortex (oxeas loosely arranged) | – | – | 4 | AN |
| *Levantiniella* Carella et al., 2016 | – | + (small, rounded) | – | 1 | AN |

**Table 2.** Number of samples reviewed per taxon. The column "Indonesia" refers to all samples recently collected in Indonesia (years 2006–2011), "other material" to older specimens in museum collections from Indonesia or other countries; "types" refer to type specimens of valid species and junior synonyms.

| Species | Indonesia | Other material | Types | Total |
|---|---|---|---|---|
| *Paratetilla bacca* | 38 | 4 | 4 | *46* |
| *Paratetilla arcifera* | 21 | 4 | 1 | *26* |
| *Cinachyrella australiensis* | 117 | 3 | 9 | 129 |
| *Cinachyrella porosa* | 47 | – | 5 | 52 |
| *Cinachyrella paterifera* | 14 | – | 1 | 15 |
| Total | 237 | 11 | 20 | **268** |

## Morphology

Radial and superficial histological sections of sponges were hand cut with a surgical blade; tissue sections were dried on a heat-plate more than 1 hour, mounted in Durcupan ACR resin and examined using light microscopy. Spicule preparations were made by dissociation of a fragment of sponge in sodium hypochlorite and consecutive washing steps, three times in distilled water, twice in 70% ethanol, and suspending in 95% ethanol. The dissociated spicules were dropped onto glass microscope slides, dried and mounted in Durcupan for light microscopy. Spicule preparations for Scanning Electron Microscopy (SEM) were made after two extra washing steps with 95% ethanol. Spicule dimensions and character definitions follow Rützler (1987), Rützler and Smith (1992) and van Soest and Rützler (2002). Spicule dimensions are based on 25 measurements for type specimens and for reference material. Data are given as minimum–mean–maximum in the text.

## Results and discussion

### Systematic descriptions

**Order Astrophorida**
**Family Tetillidae Sollas, 1888**
**Genus *Paratetilla* Dendy, 1905**

The genus *Paratetilla* was established by Dendy (1905) based on the presence of a layer of modified triaenes (calthrops-like). Eleven nominal species have been described with this diagnostic character: *Stelletta bacca* Selenka, 1867, *Tethya merguiensis* Carter, 1883, *Tetilla ternatensis* Kieschnick, 1896, *Tetilla amboinensis* Kieschnick, 1898, *Tetilla violacea* Kieschnick, 1898, *Tetilla rubra* Kieschnick, 1898, *Paratetilla cineriformis* Dendy, 1905, *Paratetilla eccentrica* Row, 1911, *Paratetilla aruensis* Hentschel, 1912, *Paratetilla corrugata* Dendy, 1922, and *Paratetilla lipotriaena* de Laubenfels, 1954. The revision of the taxonomic history of these species reveals that some ambiguous statements have been made (Table 3).

Recent checklists and biodiversity studies in the Indo-Pacific have only recorded *P. bacca*, following Burton's taxonomic decision in 1959 to synonymize all nominal *Paratetilla* species except *P. lipotriaena*. Two exceptions were found in the literature, the review by Desqueyroux-Faundez (1981) of Topsent's material (1897) from Amboina Island, who identified it as *Paratetilla merguiensis*, and the inventory of sponges from South China Sea by Hooper et al. (2000), where *P. arcifera* was listed in addition to *P. bacca*.

**Table 3.** Historic milestones in the taxonomy of the genus *Paratetilla* Dendy, 1905. Asterisk (*) indicates misidentification of *Cinachyrella* specimens as *Paratetilla*.

| Year | Author | Descriptions / Statements |
|---|---|---|
| 1867 | Selenka | Description of *Stelletta bacca*. Selenka's material was collected in Samoa Island and due to the presence of triaenes this species was associated to the family Corticatae (now Astrophorida: Ancorinidae). The description is brief but the sketches included are illustrative, including "Vierstrahler" (=calthrop-like) spicules. Sigma-like spicules are neither mentioned in the description nor drawn in the figures. Currently, type specimen could not be located. |
| 1883 | Carter | Description of *Tethya merguiensis*, including sigmaspires, calthrop-like spicules, oxeas and triaenes and their respective measurements and sketches. |
| 1884 | Ridley | In his monograph, Ridley kept *Stelletta bacca* in the genus *Stelletta*. The diagnostic characteristic for *Stelletta* for his decision was the absence of bacillar or acerate flesh-spicules. He also noticed that the Samoan *Stelletta* "is probably a *Tethya*, as its stellate agrees with the large stellate of that genus, and its forks are rare and probably foreign to the sponge" (see footnote in Ridley 1884, p. 472). |
| 1887 | Vosmaer | Statement about *Stelletta bacca* mentioning that it can hardly belong to *Stelletta* genus without further argumentation. |
| 1888 | Sollas | Establishment of Family Tetillidae, type genus *Tetilla* Schmidt, 1868. Sponges in this family have sigmaspires (microscleres) and slender protriaenes (megascleres) as diagnostic characters. In this family Sollas included the species *Craniella (Alcyonium) cranium* Müller (1789), species under the genus *Tethya* by Lamarck (1815) and Gray (1867), and species within the group Tethyina Carter (1875). Carter's material of *Tethya merguiensis* was redescribed and transferred to the genus *Tetilla*, as *Tetilla merguiensis*. *Tethya cranium* var. *australiensis* was redescribed as *Tetilla* (?) *australiensis*. Many other species were also described by Sollas within this family. |

| Year | Author | Descriptions / Statements |
|---|---|---|
| 1896* | Kieschnick | Description of *Tetilla ternatensis* based on material from Ternate Island (Indonesia); he mentioned "Vierstrahler" (=calthrops). |
| 1897 | Lindgren | *Tethya merguiensis* Carter, 1873 as junior synonym to *Stelletta bacca*, based on a comment by Sollas (1888, p. 205) of his monograph: "*Stelletta bacca*, Selenka, which Vosmaer correctly excludes from *Stelletta*, while Ridley includes it, is as mounted preparations show, identical with *Tetilla merguiensis*, Carter". However, neither Ridley (1884) nor Vosmaer (1887) supported their inclusion or exclusion of the species with any description of the Selenka specimen, but apparently, they were based merely on the published description. It is remarkable that Sollas in the same monograph (1888) identified the Challenger specimens as *Tetilla merguiensis*, including for the first time this genus and species under the family Tetillidae due to the characteristic sigmaspires. |
| 1898* | Lindgren | Redescription of *Tetilla bacca*, with *Tetilla merguiensis* as junior synonym, including material of Torres Straits (North Australia), two localities at Java (Indonesia) and Carter's specimens from Mergui Archipelago. Size range for each station is shown for oxeas and triaenes, arguing that larger spicules are found to the west while smaller sizes to the east. Redescription of *Tetilla ternatensis* based on Java material. It is remarkable that he mentioned the presence of numerous microxeas (240 × 4 µm) and sigmaspires 24 µm. |
| 1898 | Kieschnick | Description of *Tetilla amboinensis*, *Tetilla violacea* and *Tetilla rubra* from Amboina Island, all of them with "Vierstrahler" (=calthrop-like) spicules. *T. amboinensis* and *T. violacea* with calthrops in a layer below the surface of the sponge; while the former is characterized by smaller number of triaenes and bundles of oxeas up to the surface of the sponge, the latter by very abundant triaenes, bundles of oxeas projected over the surface of the sponge, and a typical violet color. *T. rubra* separated from the other two by its brick-red color and with calthrops mainly on the basal part of the sponge. |
| 1900 | Kieschnick | Extensive description of the same three new species. |
| 1900* | Thiele | Redescription of *Tetilla ternatensis* Kieschnick, 1896. Thiele drew attention on the misidentification of *T. ternatensis* by Lindgren (1898), clarifying that Lindgren specimens exhibited microxea resembling *Tetilla australiensis* (Carter, 1886). Moreover, Thiele proposed that *T. ternatensis*, as well as Kieschnick's species *T. amboinensis*, *T. violacea* and *T. rubra*, should be junior synonyms of *T. bacca* arguing that *T. bacca* shows a large morphological variability. |
| 1900* | Kirkpatrick | Extension of the geographical range of *T. bacca* and *T. ternatensis* to Christmas Island. *T. bacca* specimens were described with identical spicules to Lindgren's (1898) material from Java. *T. ternatensis* also similar to Lindgren's (1898) material of *T. ternatensis.* |
| 1903* | Lendenfeld | Designation of a new species *Tetilla lindgren*i based on Lindgren's specimens (1898) from Java and Kirkpatrick's specimens (1900) from Christmas islands, both identified as *T. ternatensis* without calthrops and with small microxeas. Thus, Lendenfeld concluded that those specimens belong to a new species *(T. lindgren*i) because they did not show calthrops as in the original description of Kieschnick (1896). Junior synonyms for *Tetilla bacc*a, including the material of Selenka, Carter, Sollas, and Kirkpatrick. *T. ternatensis* and *T. violacea* described by Kieschnick and recorded by Thiele (1900) were also included as junior synonyms of *T. bacca*. *Tetilla amboinensis* Kieschnick (1898) was transferred to genus *Cinachyra* and *T. rubra* was established as its junior synonym. |
| 1905 | Dendy | The genus *Paratetilla* was erected within the family Tetillidae, based on the presence of calthrop-like spicules. Thus, *Tetilla bacca* is transferred to *Paratetilla* genus, including their junior synonyms *T. merguiensis,* as well as the three Kieschnick's species *T. ternatensis*, *T. amboinensis* and *T. violacea* based on Thiele's annotation (1903). Description of *Paratetilla cineriformis* based on material from Gulf of Manaar (Sri Lanka). Although the spicules shown by *P. cineriformis* resembled *T. merguiensis*, Dendy (1905) argues that the general aspect of the sponge was quite different as porocalices have no specific arrangement and the layer of calthrops was more irregular than in Carter's species. |
| 1907 | Lendenfeld | The genus *Amphytethya* was created based on its characteristic amphitriaenes. Many other species under the genus *Cinachyra*, *Fangophilina* and *Tetilla* were described. |
| 1911 | Row | Description of *Paratetilla eccentrica* from the Red Sea. Cortical triaenes (= calthrop-like) with high modifications, in some cases even becoming into "walking-sticks". |
| 1912 | Hentschel | Description of *Paratetilla aruensis* from Aru- and Kei- Islands (Indonesia), with characteristic amphitriaenes. Relocation of the genus *Amphitethya* Lendenfeld, 1907 as a junior synonym of *Paratetilla*. |

| Year | Author | Descriptions / Statements |
|---|---|---|
| 1922 | Dendy | All nominal species with calthrop-like spicules were synonymized to *Paratetilla bacca*, except for *P. aruensis* Hentschel, 1912. Two varieties were identified: *P. bacca* var. *violacea* based on *T. violacea* characteristics, and the new variety *P. bacca* var. *corrugata* from Diego Garcia in the Indian Ocean. |
| 1925 | Wilson | Description of *Paratetilla arcifera* from Philippines. Wilson recognized as valid four additional species: *P. bacca* (Selenka, 1867), *P. amboinensis* (Kieschnick, 1898), *P. cineriformis* (Dendy, 1905) and *P. eccentrica* (Row, 1911). However, he also commented that *P. bacca* is a comprehensive variable species, as previously proposed by Thiele (1903) and later established by Dendy (1922). Establishment of *Cinachyrella* genus. Validation of the genus *Amphitethya* Lendenfeld, 1907. |
| 1954 | de Laubenfels | Description of *Paratetilla lipotriaena* from Micronesia (West-Central Pacific), characterized by variable calthrop-like spicules and the absence of triaenes, and relatively similar to *P. eccentrica* Row, 1911. |
| 1959 | Burton | All nominal species described within the genus *Paratetilla* were included as synonyms of *P. bacca*, except for *P. lipotriaena*. |
| 1987 | Rützler | Review of Family Tetillidae, including seven genera (all except for *Fangophilina*). Nomination of *Paratetilla cineriformis* as type species of genus *Paratetilla*. |
| 1994 | Hooper and Wiedenmayer | Review of all *Paratetilla bacca* synonyms based on Burton (1959) taxonomic decision. |
| 2002 | van Soest and Rützler | Review of the eight genera included within family Tetillidae. Although *Paratetilla* characters were a combination of two descriptions, a paragraph in the discussion included the size differences between both Selenka's and Carter's material (*Stelletta bacca* and *Tethya merguiensis*, respectively). The origin of calthrop-like spicules was also discussed as probably modified plagiotriaenes resembling some *Cinachyrella* species, arguing the possibility of the inclusion of the widespread species *Paratetilla bacca* within *Cinachyrella* genus. |
| 2008 | van Soest and Beglinger | Redescription of *Paratetilla corrugata* based on material from the Gulf of Oman, and giving validity to the variety *P. bacca* var. *corrugata* by Dendy (1922). The presence of trichodragmata is characteristic of this species. |
| 2018 | van Soest et al. (WPD) | Junior synonyms for *Paratetilla bacca* (Selenka, 1867): *Tetilla bacca* (Selenka, 1867), *Stelletta bacca bacca* Selenka, 1867, *Tethya merguiensis* Carter, 1883, *Stelletta bacca* Selenka, 1887, *Tetilla violacea* Kieschnick, 1896, *Tetilla ternatensis* Kieschnick, 1896, *Tetilla rubra* Kieschnick, 1898, *Paratetilla cineriformis* Dendy, 1905, *Paratetilla eccentrica* Row, 1911, *Paratetilla arcifera* Wilson, 1925. Other accepted *Paratetilla* species in WPD: *Paratetilla amboinensis* (Kieschnick, 1898), *Paratetilla aruensis* Hentschel, 1912, *Paratetilla corrugata* Dendy, 1922, *Paratetilla lipotriaena* de Laubenfels, 1954. |
| 2018 | This study | *Paratetilla* species from Indonesia: *Paratetilla bacca* (Selenka, 1867), *Paratetilla arcifera* Wilson, 1925, and *Paratetilla corrugata* Dendy, 1922 (not observed in our Indonesian material), *Paratetilla aruensis* Hentschel, 1912 with amphitriaenes, it is suggested to be transferred to *Amphitethya*. |

## ***Paratetilla bacca*** **(Selenka, 1867)**

Figs 1, 2

*Stelletta bacca* Selenka, 1867: 569, pl. xxxv, figs 14, 15 (type not found, material from type locality seen).

*Tethya merguiensis* Carter, 1883: 366, pl. xv, figs 6–8; Carter, 1887: 80 (type seen).

*Tetilla merguiensis*; Sollas, 1888: 14; Topsent, 1897: 441, pl. xviii, fig. 4–5, pl. xxi figs 34.

*Tetilla ternatensis* Kieschnick, 1896: 527. Thiele, 1900: 39, pl. ii, fig 13; Not *Tetilla ternatensis* Lindgren, 1898: 329 pl. 17, fig. 14; pl. 19, Fig. 25 a-e, a', b'.

*Tetilla bacca*; Lindgren, 1897: 485; Lindgren, 1898: 328; Thiele, 1900: 39, pl. ii, fig 13; Kirkpatrick, 1900: 132 (material seen); Lendenfeld, 1903: 19.

*Tetilla amboinensis* Kieschnick, 1898: 10.
*Tetilla violacea* Kieschnick, 1898: 15.
*Tetilla rubra* Kieschnick, 1898: 18.
*Paratetilla cineriformis* Dendy, 1905: 97, pl. iii, fig. 7 (type seen).
*Paratetilla eccentrica* Row, 1911: 306, pl. xxxv, fig. 1, pI. xxxvi, fig. 8 (type seen).
*Cinachyra amboinensis*; Hentschel, 1912: 331.
*Paratetilla bacca*; Dendy, 1922: 21 (material seen).
*Paratetilla bacca* var. *violacea*; Dendy, 1922: 22, pl. 1, fig. 6 (material seen).
*Paratetilla lipotriaena* de Laubenfels, 1954: 244, text figure no. 168 (type seen).

**Material examined.** Neotype ZMA.POR.13029, Tutuila Island, American Samoa. Holotype of first junior synonym *Tethya merguiensis* Carter, 1883 (?) NHMUK 1894.11.16.17, Mergui Archipelago, Myanmar. Holotype NHMUK 1954.2.23.106 Gulf of Manaar, Sri Lanka (as *Paratetilla cineriformis* Dendy, 1905). NHMUK unreg. type, Crossland Collection, Red Sea (as *Paratetilla eccentrica* Row, 1911). NHMUK 1898.12.20.19, Flying Cove Fish, Christmas Islands (as *Tetilla bacca=Paratetilla merguiensis* Kirkpatrick, 1900). NHMUK 1921.11.7.10, Sealark Sponges, Indian Ocean (as *Paratetilla bacca* var. *violacea*). Holotype USNM 23049, East part of Lagoon, Ponape, Caroline Islands, 1 Aug 1949 (as *Paratetilla lipotriaena* de Laubenfels, 1954). **INDONESIA**. Bali, *Bali reef,* RMNH.POR.1732; East Kalimantan, *Berau reef,* RMNH.POR.11281, RMNH.POR.11282, RMNH.POR.11283; *Kakaban Lake,* RMNH.POR.11289, RMNH.POR.11290, RMNH.POR.11291, RMNH.POR.11292, *Haji Buang Lake,* RMNH.POR.11284, RMNH.POR.11287, RMNH.POR.11288, RMNH.POR.11285, RMNH.POR.11286, RMNH.POR.3515. Sulawesi, *Bunaken reef,* RMNH.POR.3100, RMNH.POR.3106, RMNH.POR.3115; *Bunaken mangrove,* RMNH.POR.2819; *Spermonde Archipelago,* ZMA.POR.13221. Ternate, *Ternate reef,* RMNH.POR.5344, RMNH.POR.5467. West Papua, *Wallace Lake,* RMNH.POR.11293, RMNH.POR.11294, RMNH.POR.11295; *Outside Wallace Lake,* RMNH.POR.11296, RMNH.POR.11297, RMNH.POR.11298; *Ctenophore Lake,* RMNH.POR.11302; *Gam Mangrove,* RMNH.POR.11299, RMNH.POR.11300, RMNH.POR.11301; *Outside Ctenophore Lake,* RMNH.POR.11303; *Big Caulerpa Lake,* RMNH.POR.11304; *Gam Island,* RMNH.POR.11305, RMNH.POR.11306, RMNH.POR.11307.

**Other material**: East Kalimantan, *Makassar Straits,* ZMA.POR.1735, Siboga Expedition, St. 81. Singapore, RMNH.POR.2506, RMNH.POR.2512. Western Indian Ocean, ZMA.POR.20673.

**Description.** ***External morphology.*** Globular sponges, size between 1 and 5 cm in diameter. Surface hispid due to the projecting spicules, covered by numerous porocalices (Figure 1A, B). Porocalices are bowl-shape, with oval to circular apertures, up to 5 mm in diameter and 7 mm deep, numerous, scattered uniformly over the surface of the sponge; in preserved material, some porocalices are closed and only a narrow aperture is visible giving to the sponge a rough appearance. External color generally brown when alive, which turns dark brown in ethanol, choanosome light brown, and

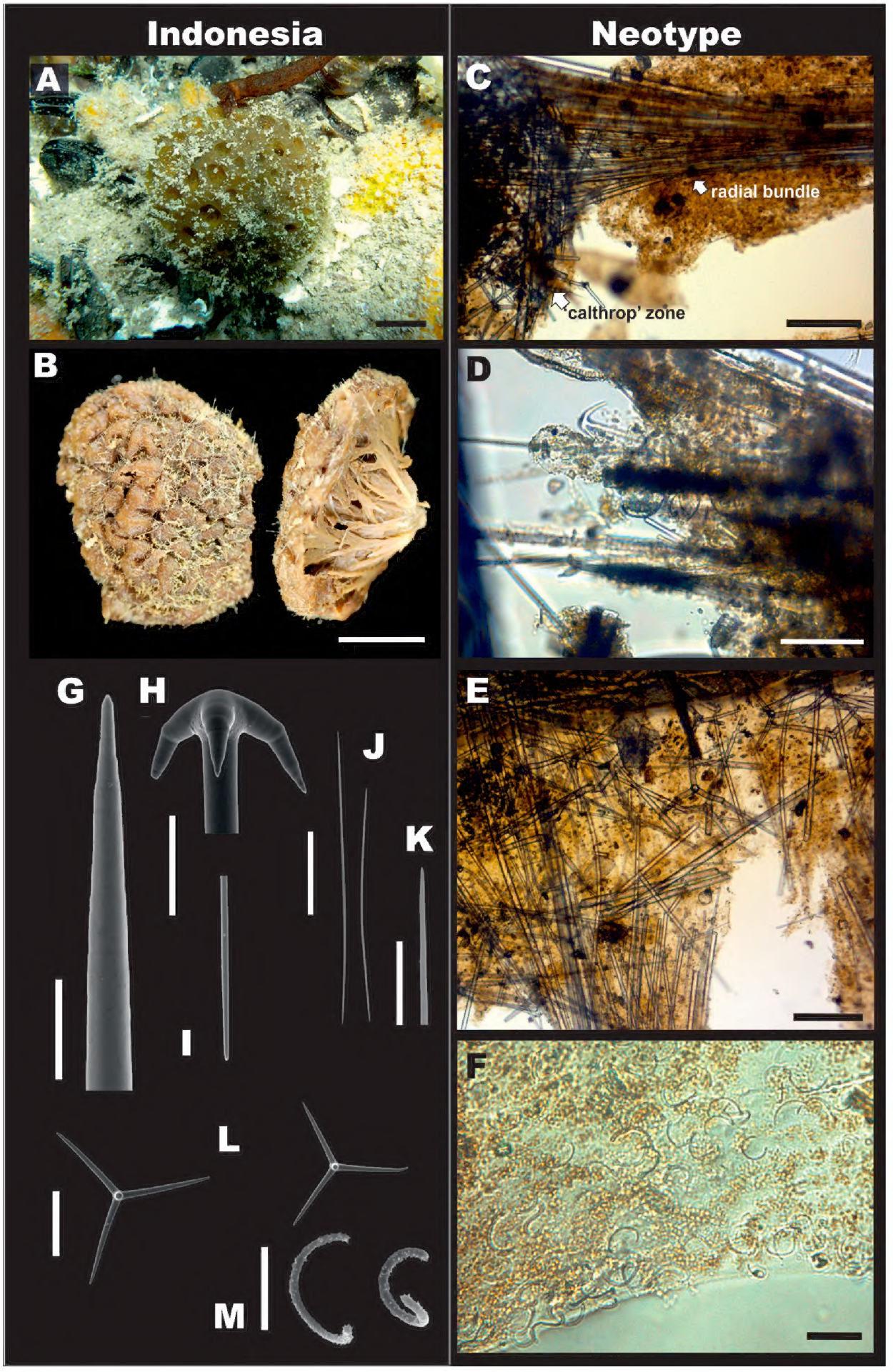


**Figure 1.** *Paratetilla bacca*. **A,B, G-M** RMNH.POR.11292, Kakaban Lake, Indonesia (left side). **C–F** neotype material of *Paratetilla bacca*, ZMA.POR.13029, Tutuila Island, American Samoa (right side). **A** *in situ* photograph **B** preserved specimen showing the porocalices (scale bar 1 cm) **C** skeleton showing oxeas, calthrops and triaenes **D** skeleton, showing anatriaenes, protriaenes and oxeas **E** skeleton showing detail of the 'calthrop' zone **F** sigmaspires **G** oxea, detail **H, I** anatriaene, cladus and rhabd end, **J** thin microxea, **K** thin microxea, detail **L** calthrops **M** sigmaspires. Scale bars: 200 µm (**A–C**); 40 µm (**D, G–I**); 200 µm (**E**); 20 µm (**F**); 50 µm (**J**); 10 µm (**K, M**); 100 µm (**L**).

has a 'dried out' appearance (Figure 1B). Numerous small dark brown granules in the tissue (Figure 1E, F). Consistency compact.

**Skeleton.** No cortex. Choanosomal skeleton composed by bundles of oxeas and triaenes radiating from a central core, ⅕–⅓ of the diameter of the sponge.

**Megascleres.** The material from Indonesia and the type of *P. merguiensis* have oxeas 850–3085.3–4500 µm × 5–41.5–65 µm (Table 4, Figure 1E, D, G). Anatriaenes always present, very abundant, cladi stout, slightly flattened, 20–62.6–100 µm × 12.5–48.3–75 µm, long rhabd up to 6000 × 20 µm, tapering to dimensions much less than 1µm (Figure 1H, I). Protriaenes scarce in some specimens and absent in the type specimen; when present, they exhibit two different shapes, the first one with stouter and smaller cladi, the second one with thinner and larger cladi (27.5–53.9–100 µm × 37.5–107.4–200 µm × 2.5–6.5–12.5 µm), rhabd up to 5850 × 15 µm, tapering to dimensions of < 1 µm. Calthrop-like short shafted triaenes, three types are distinguished with a wide range of sizes, from which measurements are shown as a general summary (Table 4). In the first type, four rays can be recognized (Figure 1L), three of them large, up to 400–600 µm, and a short one up to 100 µm long, usually pointing down to the centre of the body; the second one with three rays, almost the same length up to 400 µm; and the third one with three rays as well, two of them in an angle of 180° and the other one perpendicular, 50–100 µm. The calthrops are located immediately below the surface, constituting more or less a homogeneous layer.

**Microscleres.** Thin microxeas are common, 105–241.6–380 µm, 'hair-like'. Sigmaspires, 10–14.1–25 µm, C-S shape (Figure 1F, M).

**Ecology.** Inhabiting all studied environments in Indonesia, including coral reefs, mangroves, and marine lakes. Specimens more common in mangroves and marine lakes, and shallow reef flats where they are usually found on dead coral skeletons or coral rubble, typically ranging in depth from 0–5m. No specimens collected from deeper coral reefs in Indonesia.

**Distribution.** *Paratetilla bacca* has a wide distribution in Indonesia, including Berau, Bunaken, Raja Ampat, Ternate, and Java. Previous Indonesian records are from Spermonde Archipelago (Becking et al. 2006), Berau (de Voogd et al. 2009), and Raja Ampat (Becking 2008). In addition, this species has also been reported from Seychelles Islands (Thomas 1973), Southwest Madagascar (Vacelet et al. 1976), Zanzibar (Pulitzer-Finali 1993), Thailand (Putchakarn 2007), Singapore (Lim et al. 2008), Philippines (Longakit et al. 2005) (Figure 2).

**Remarks.** We did not succeed in locating the holotype of *Paratetilla bacca*, despite concerted effort. At this time, we assume that the type is no longer available. The description by Selenka of the type specimen does not mention the occurrence of any type of sigmaspires. It is a matter of speculation whether Lindgren (1897) actually examined Selenka's material to propose Carter's species *Paratetilla merguensis* as a junior synonym to *Paratetilla bacca*, or whether he based his conclusion merely on the literature. It is possible that sigmaspires may have been overlooked by Selenka in his original description and drawings, yet the arrangement of the megascleres in the skeleton shows a clear similarity with Carter's species *P. merguensis* (Suppl. material 2, Figure S1). In contrast

to Selenka's description, Carter (1883) included a complete and detailed account of *P. merguiensis*, which was verified through examination of two slides deposited in the NHM collection (NHMUK 1894.11.16–17); few oxeas are complete in these slides (most broken), therefore limited variation of this character was observed. For most of spicule types enough measurements were possible. Although we did not succeed finding Selenka's type, we did examine one specimen and its associated slide preparation from Samoa identified as *P. bacca* (ZMA.POR.13029), which has all the characteristic spicules, including sigmaspires, that are present in our specimens from Indonesia (Figure 1C-F). This material is designated here with the status of neotype following the rules of the International Code of Zoological Nomenclature, article 75. Therefore, we conclude that *P. bacca* is a valid species, and subsequent species should be designed as junior synonyms. In all of our *Paratetilla* samples, we have furthermore not encountered one specimen without sigmaspires. Here, we show the measurements of the holotype of *P. merguiensis*, as well as specimens from different localities in Indonesia (Table 4). Although there is a large variation in spicules sizes among the different localities, there was also great intra-specific variation and we did not find any reason to declare the validity of any junior synonym included in this revision. In general, populations from marine lakes (Kakaban and Haji Buang) exhibit smaller spicules in comparison with their reefal counterparts at the same localities (Table 4). This variation could be a response to different environmental conditions within the marine lakes (Becking et al. 2011), or a consequence of genetic selection after isolation of these populations about 8000–10000 years ago (Dawson and Hamner 2005, Becking et al. 2013, Becking et al. 2016), or a synergistic effect between environmental and genetic factors.

According to the WPD (van Soest et al. 2018), other four valid *Paratetilla* species are *P. amboinensis* (Kieschnick, 1898), *P. lipotriaena* de Laubenfels, 1954, *P. corrugata* Dendy, 1922 and *P. aruensis* Hentschel, 1912. Based on the description of *P. amboinensis* (Kieschnick, 1898), the shape and skeleton features exhibited by this species fit within the current diagnosis of *P. bacca*, therefore we recommend that these two species should be synonymized. The species *P. lipotriaena* was erected by de Laubenfels based on the absence of triaenes. Our examination of the type specimen (USNM 23049) revealed the presence of triaenes and the same characters as *P. bacca*, therefore we have synonymized this species with *P. bacca.* On the other hand, *P. bacca* can be distingished from *P. corrugata* Dendy, 1922, because of the abundant trichodragmata exhibited by the latter species. Consequently, *P. corrugata* can still be considered a valid species. Finally, the status of *P. aruensis* Hentschel, 1912 within this genus should be reconsidered. After examination of two slides available at the NHMUK, no calthrops were found, only the typical amphitriaenes originally described for this species. Amphitriaenes make this species more similar to the genus *Amphitethya* instead of *Paratetilla*. Further examination of specimens would corroborate our preliminary conclusion.

In a molecular phylogenetic study, which was based in part on specimens that we review in the current study (see Suppl. material 1, Table S1 for corresponding GenBank numbers), Schuster et al. (2017) distinguishes *P. bacca* as a monophyletic clade in the Tetillidae. Due to the wide distribution of this species and large intraspecific

**Table 4.** Spicule measurements of six specimens of *Paratetilla bacca* and five specimens of *P. arcifera* from different regions (n = 10 per spicule type and dimension with minimum-**mean**-maximum). Asterisk (*) indicate that rhabds of spicules were broken and no measurement was possible.

| Measurements | | *Paratetilla bacca* | | | | | | *Paratetilla arcifera* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **NHMUK94.11.16.17/16** | **RMNH.POR.11292** | **RMNH.POR.11287** | **RMNH.POR.11281** | **RMNH.POR.11301** | **RMNH.POR.5344** | **USNM21278 (Holotype)** | **RMNH.POR.11266** | **RMNH.POR.11273** | **RMNH.POR.11310** | **RMNH.POR.3114** |
| **Locality** | | Mergui Archipelago | Kakaban Lake | Haji Buang Lake | Berau | Raja Ampat | Ternate | Philippines | Berau | Berau | Ternate | Manado |
| **Habitat** | | Reef | Marine Lake | Marine Lake | Reef | Mangrove | Reef | Reef | Reef | Reef | Reef | Reef |
| **Oxeas** | Length | 3114.**36**–**3114**.6–3115 | 8**50**–**2340.8**–3150 | 1000–2922–3850 | 2520–**3324.6**–3850 | 3100–3270–3500 | 1250–3540–4500 | 1650–2435–3125 | 1650–3093–4500 | 1600–3041–4175 | 840–1996–3100 | 3100–3600–4000 |
| | Width | 40.8–**42.5**–51 | 5–**29.9**–40 | 12.5–36–50 | 30–**48.8**–60 | 30–42–55 | 25–49.6–65 | 20–39.5–65 | 25–42.2–55 | 20–33.7–50 | 10–25.4–50 | 27.5–43–52.5 |
| **Anatriaenes** | Rhabd length | * | 3000–**3677**.8–4600 | 3900–4741.7–5300 | 4250–**5057**.1–6000 | * | * | * | * | * | * | * |
| | Rhabd width | 15–**16**–20 | 5–**12**.9–20 | 12.5–**14.8**–17.5 | 7.5–**10.7**–15 | 7.5–11.3–15 | 5–7.5–10 | * | * | * | 5–5.7–7.5 | 5–6.3–7.5 |
| | Cladi total | 20–**27.9**–40 | 37.5–**58.7**–75 | 80–**91.5**–100 | 40–73.6–90 | 60–74.5–80 | 22.5–49.5–75 | 40–68–80 | 60–65.6–80 | 22.5–39.8–60 | 40–48.2–50 | 50–65–75 |
| | Cladi length | 40.8–**52**–71.4 | 25–**44.4**–65 | 50–**63.9**–75 | 20–40.5–50 | 40–57.3–75 | 12.5–31.8–50 | 25–39.4–45 | 30–38.7–47.5 | 10–21.3–30 | 15–20.9–25 | 35–40.6–50 |
| | Cladi width | 10–**12**–15 | 7.5–**12.1**–20 | 7.5–**10.9**–15 | 7.5–10.7–15 | 7.5–9.5–10 | 5–7-7.5 | 5–8.2–10 | 5–6.6–10 | 2.5–5-7.5 | 5–5-5 | 5–6.3–7.5 |
| **Protriaenes** | Rhabd length | * | 3900–**3900**–3900 | 3000–**4434**.6–5850 | 3100–3800–4500 | * | * | * | * | * | * | * |
| | Rhabd width | * | 7.5–**10**–12.5 | 10–**13**.3–17.5 | 5–8.6–15 | 2.5–4.8–5 | 5–5-5 | * | * | * | * | 5–6-7.5 |
| | Cladi total | * | 27.5–**46**.9–70 | 40–**70**.7–100 | 50–67.9–100 | 30–54–70 | 30–30–30 | * | 30–38.3–40 | 40–40–40 | * | 30–42.8–50 |
| | Cladi length | * | 47.5–**84.4**–100 | 85–**140.5**–185 | 110–141.4–200 | 50–133–170 | 37.5–37.5–37.5 | * | 50–61.7–70 | 75–75–75 | * | 25–40.3–60 |
| | Cladi width | * | 5–**7.5**–10 | 7.5–**9.5**–12.5 | 5–7.9–10 | 2.5–2.5–2.5 | 5–5-5 | * | 2.5–5.4–7.5 | 5–5-5 | * | 2.5–4.3–5 |
| **Calthrops** | C1 | 42.5–**168**.1–255 | 110–**266**–475 | 270–**369**.8–510 | 140–296.7–360 | 220–301–350 | 250–375.7–600 | 320–362.5–430 | 150–253.9–375 | 110–154–220 | 150–192.5–250 | 120–179–220 |
| | C2 | 22.5–**92**.9–183.6 | 90–**225**–325 | 220–**346.4**–460 | 140–281–350 | 210–284–350 | 240–291.4–350 | 230–287.5–320 | 75–239.4–390 | 90–134.4–160 | 70–125–230 | 90–129–200 |
| | C3 | 20–**106**–234.6 | 40–**203.7**–325 | 50–**292.5**–400 | 25–218.7–345 | 180–254–310 | 200–272.9–350 | 120–195–300 | 140–245.5–355 | 60–110–150 | 50–93.3–160 | 90–129–200 |
| | Width | 3.5–**12.2**–20.4 | 7.5–**18.3**–35 | 15–**31.7**–45 | 10–18.3–27.5 | 10–14.5–17.5 | 17.5–20.4–25 | 15–18.8–22.5 | 10–18.3–25 | 10–12.5–15 | 10–13.8–17.5 | 12.5–15–20 |
| **Microxea** | | 173.4–**195**.3–224.4 | 105–**136**.2–212.5 | 170–**213**.6–250 | 250–316.8–385 | 210–264–300 | 250–323.6–380 | 180–308.4–380 | 270–323.2–400 | 200–342–500 | 340–370–410 | 250–367–450 |
| **Sigmaspires** | | 12.5–**14**.4–17.5 | 10–**13**–17.5 | 12.5–**15**.4–25 | 12.5–14.2–17.5 | 12.5–13.8–15 | 12.5–14–17.5 | 7.5–12.5–17.5 | 12.5–15.4–17.5 | 15–16.3–20 | 12.5–15.3–17.5 | 12.5–14–17.5 |

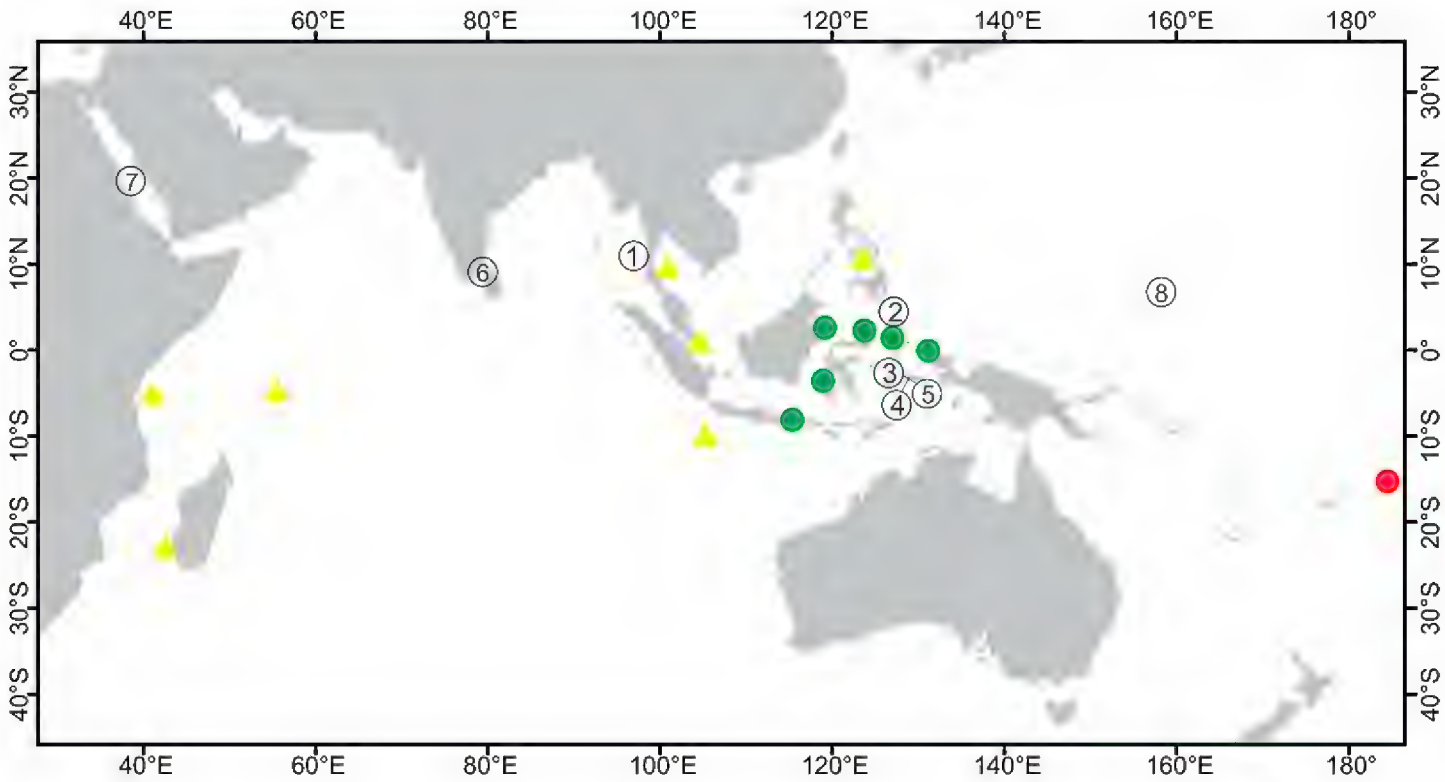


**Figure 2.** Distribution of *Paratetilla bacca*. Red dot: type locality, *Stelletta bacca* Selenka, 1867, American Samoa. Green dots: Indonesian localities where the species was collected recently. Yellow triangles: Records from localities outside Indonesia, Zanzibar, Southwest Madagascar, Seychelles, Thailand, Singapore, Christmas Island, and Philippines. Circled numbers: type localities of synonymized species, **1** *Tethya merguiensis* Carter, 1873, Mergui Archipelago **2** *Tetilla ternatensis* Kieschnick, 1896, Ternate Island **3** *Tetilla amboinensis* Kieschnick, 1898, Ambon Island **4** *Tetilla violacea* Kieschnick, 1898, Ambon Island **5** *Tetilla rubra* Kieschnick, 1898, Ambon Island **6** *Paratetilla cineriformis* Dendy, 1905, Gulf of Manaar, Sri Lanka. **7** *Paratetilla eccentrica* Row, 1911, Tella Tella Kabira, Red Sea **8** *Paratetilla lipotriaena* de Laubenfels, 1954, Matalanim, Eastern Pohnpei, Micronesia.

morphological variability we recommend further molecular studies, particularly of *P. bacca* from its type locality (American Samoa). This would allow a more detailed description of the genetic variation of *P. bacca* and verify our initial taxonomic proposal based on morphology.

### *Paratetilla arcifera* Wilson, 1925

Figs 3, 4, 5

*Paratetilla arcifera* Wilson, 1925: 380; plate 40, fig. 2; plate 48, fig. 6 (type seen).

**Material examined.** Holotype USNM 21278, Albatross Stn. 5400, Malapascua Island, Cebu, Philippines, 46 m, 16 Mar 1909. **INDONESIA**. East Kalimantan, *Berau reef*, RMNH.POR.11131, RMNH.POR.11265, RMNH.POR.11266, RMNH.POR.11269, RMNH.POR.11267, RMNH.POR.11268, RMNH.POR.11270, RMNH.POR.11271, RMNH.POR.11272, RMNH.POR.11273. Bali, RMNH.POR.1870. Java, *Thousand Islands,* RMNH.POR. 2076. Sulawesi, *Bunaken,* RMNH.

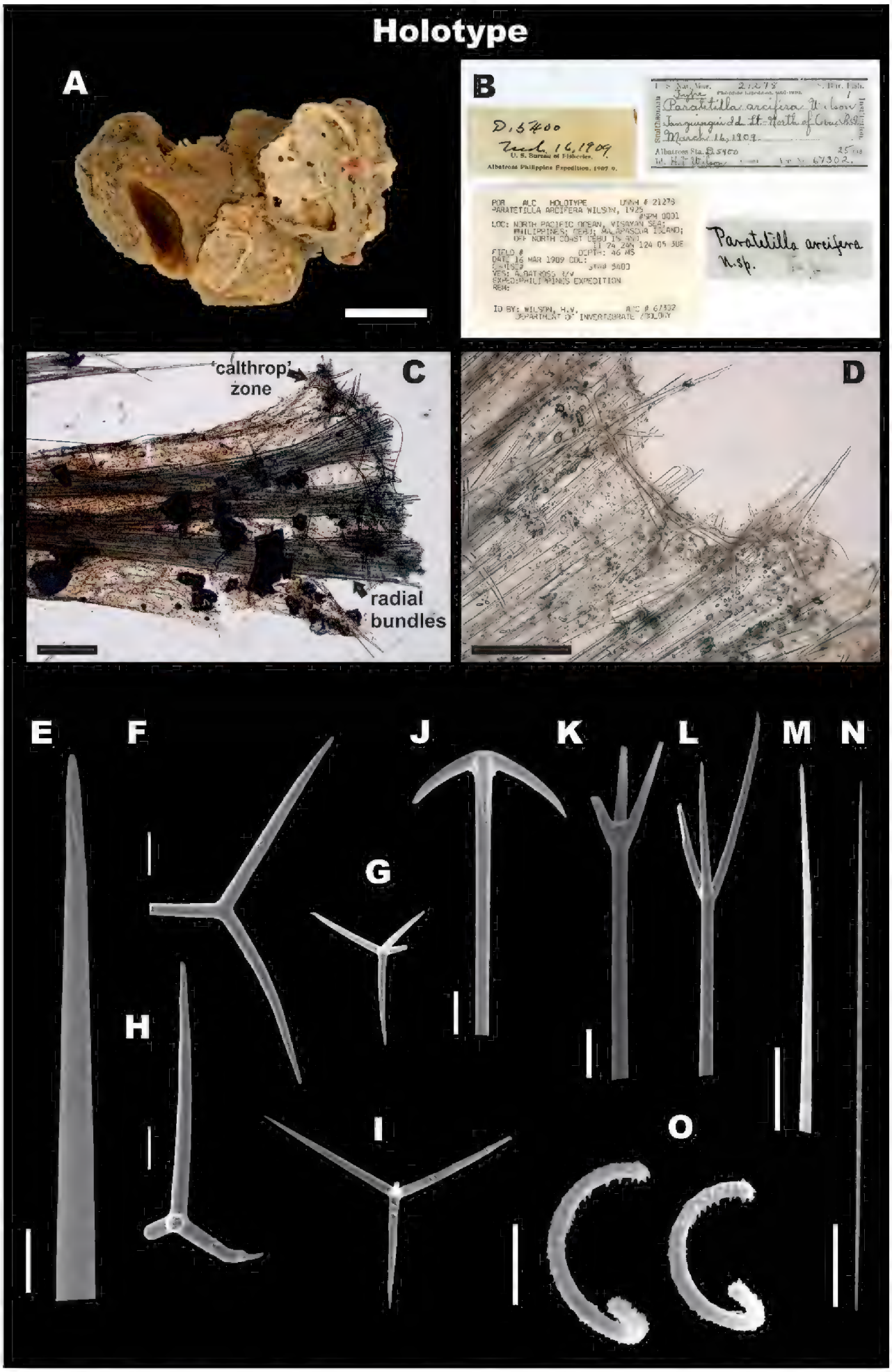


**Figure 3.** *Paratetilla arcifera*. Holotype USNM 21278, Malapascua Island, Cebu, Philippines **A** preserved specimen showing large porocalices **B** Labels of holotype **C** skeleton, showing calthrops and radial bundles **D** skeleton, showing oxeas, calthrops, and anatriaenes **E** oxea, end detail **F-I** different calthrop shapes and sizes **J** anatriaene **K, L** protriaene, different types **M** thin microxea, detail **N** thin microxea, full length **O** sigmaspires. Scale bars: 1 cm (**A**); 500 μm (**C, D**); 100 μm (**E**); 50 μm (**F–I, N**); 20 μm (**J**); 40 μm (**K, L**); 5 μm (**M, O**).

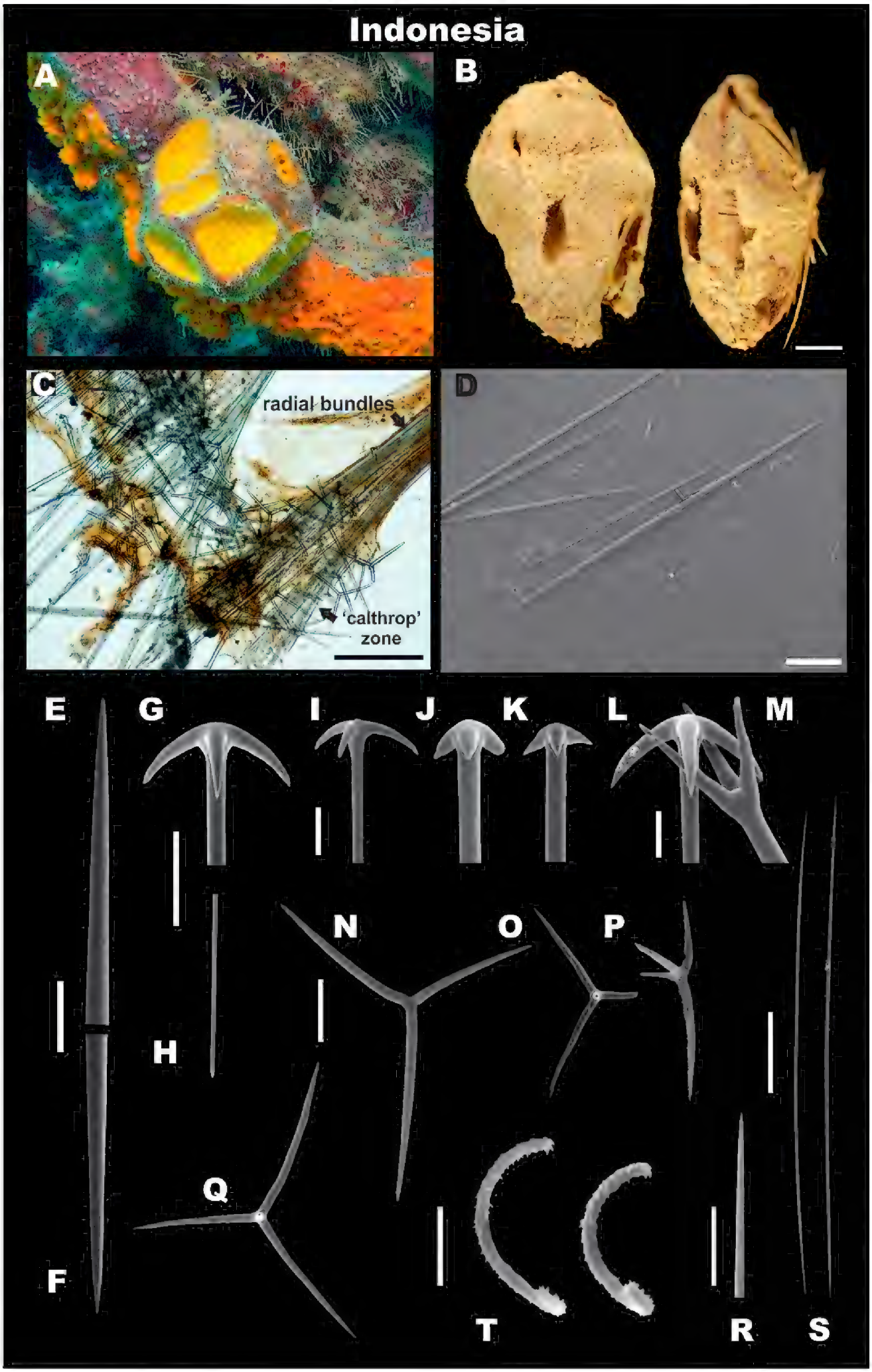


**Figure 4.** *Paratetilla arcifera* from Indonesia RMNH.POR.11266. **A** in situ photograph. **B** preserved specimen showing the porocalices (scale bar 1 cm) **C** skeleton **D** spicules **E, F** oxea, end detail **G, H** natriaene, cladus. and rhabd end **I-L** anatriaene, different types **M** Protriaene **N-Q** different calthrops **R** thin microxea, detail **S** thin microxeas, full length **T** sigmaspires. Scale bars: 1 cm (**B**), 500 µm (**C,D**), 100 µm **E,F**); 40 µm (**G,H**); 20 µm (**I–M**); 200 µm (**N–Q**); 5 µm (**R,T**); 50 µm (**S**).

POR.3114; *Manado* RMNH.POR.3114. Ternate, *Ternate reef, RMNH.POR.*11310. West Papua, *Kerupiar Island reef,* RMNH.POR.11280; *Outside Ctenophore Lake,* RMNH.POR.11275; *Gam Island,* RMNH.POR.11277, RMNH.POR.11278, RMNH.POR.11279, RMNH.POR.11274, RMNH.POR.11276. **TAIWAN**. *Reef,* RMNH.POR.3196, RMNH.POR.3206, RMNH.POR.3225, RMNH.POR.3236.

**Description. External morphology.** Globular sponges, size from 3 to 6 cm in diameter (Figs 3A, 4A). Surface hispid due to the projecting spicules, covered by numerous porocalices. Porocalices are bowl-shape, with oval apertures, up to 10 × 5 mm and 6 mm deep, few, mainly on the top surface of the sponge; in preserved material, most porocalices remained open (Figs 3A, 4A). Color generally bright orange when alive, which turns darker or even brown in ethanol. No granules in choanosome. Fleshy consistency.

**Skeleton.** No cortex. Skeleton composed by bundles of oxeas and triaenes radiating from a central core, and spaced between each other, giving a softer consistency (Figs 3C, D, 4C).

**Megascleres.** Holotype and Indonesian specimen size ranges are summarized in Table 4. Holotype: Oxeas 1650–2435–4500 µm × 20–36.8–65 µm; anatriaenes very abundant (Figure 3J), rhabds generally broken, up to 6000 × 10 µm, apparently tapering to dimensions of < 1 µm, cladi thin, slightly flattened, 40–68–80 µm × 25–39.4–45 µm × 5–8.2–10 µm; few protriaenes (Figure 3K,L), thinner and small cladi (40–65–80 µm × 60–85–110 µm), rhabds mostly broken, up to 5000 × 15 µm, tapering to dimensions of < 1 µm; two types of calthrop-like short shafted triaenes, one type with four rays of which three are short (150–300 µm) and one is large (400 µm) (Figure 3H), the other type has three rays of almost equal length up to 400 µm (Figure 3 F-G, I); calthrops are abundant in some specimens, but can be in very low numbers till almost absent in some others, they are located immediately below the surface, constituting a thin layer that can be missed in some spicule preparations.

**Microscleres.** Thin microxeas are common, 180–308.4–380 µm, 'hair-like' (Figs 3M, N, 4R, S). Sigmaspires, 7.5–12.5–17.5 µm, C-S shape (Figs 3O, 4T).

**Ecology.** Coral reef habitats at depths from 1- 20/30 m. Absent from marine lakes, mangroves and other localities with higher sedimentation and/or variable salinity.

**Distribution.** Occur in coral reefs of Berau, Bunaken, Ternate, and Raja Ampat. An additional record from its type locality, Philippines (Wilson, 1925) could be inferred from the literature (see Longakit et al. 2005: Figure 9 as *P. bacca*), and collections from Taiwan (Figure 5).

**Remarks.** Spicule sizes for most Indonesian specimens vary within the holotype ranges, except for the Ternate population, which exhibits smaller sizes and lack of protriaenes (Table 4). The typical orange color and 'fleshy' soft consistency are easy distinctive characters of this species (Figure 4A). The differences between *P. arcifera* and its congener *P. bacca* lie in the stark orange coloring, the fleshy consistency, the lack of granules, the larger porocalices, and thin microxeas generally longer than in *P. bacca*. *P. arcifera* specimens are typically larger than *P. bacca.* We, furthermore, deem *P. arcifera* a distinct species from *P. bacca,* based on recent molecular phylogenetic analyses that included *P. arcifera* (genbank accession number LT628349) and *P. bacca* (LT628350) specimens reviewed in our current study and support the hypothesis of two species (Schuster et al. 2017).

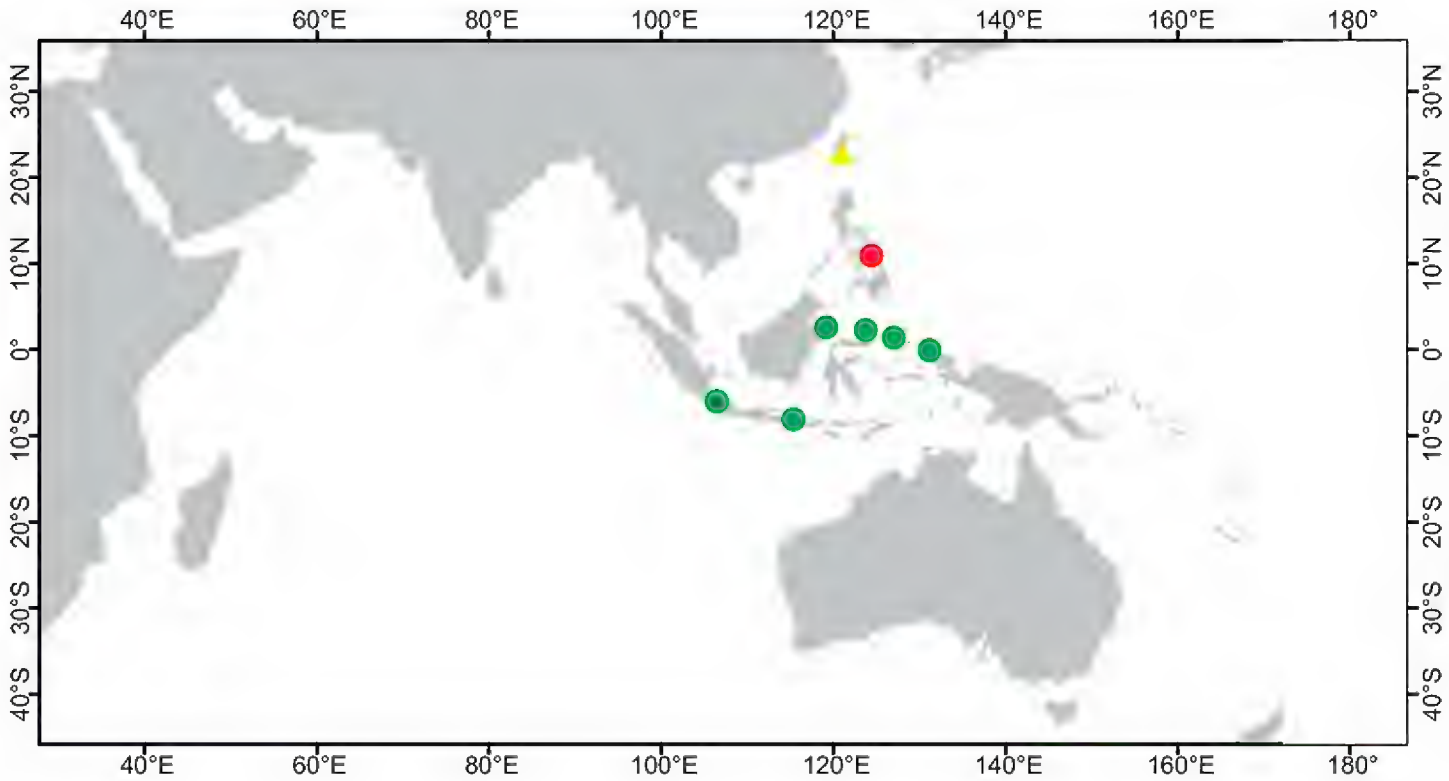


**Figure 5.** Distribution of *Paratetilla arcifera*. Red dot: type locality, *Paratetilla arcifera* Wilson, 1925, Tanguingui Island, Philippines. Green dots: Indonesian localities where the species was collected recently. Yellow triangle: Records from localities outside Indonesia, Taiwan.

## Genus *Cinachyrella* Wilson, 1925

Currently, 42 species are valid within the genus *Cinachyrella* according to the WPD (van Soest et al. 2018), including the homonyms of *C. globulosa* and one additional description of *C. cavernosa* (Lamarck, 1815) sensu Burton (1959). Originally, Wilson (1925) grouped certain species of the genera *Tetilla* and *Cinachyra* under the subgenus *Cinachyrella* based on the presence of porocalices (poriferous pits) and the absence of cortex. Subsequently, a complete review of Caribbean species by Rützler and Smith (1992) included four valid *Cinachyrella* species and it was recently complemented with the description of two new species from Brazilian deep waters (Fernández et al. 2018). The most recent review of the Indo-Pacific species was attempted by Burton (1934). In his monograph, Burton established that 16 nominal species were synonyms of the widespread and variable species *Cinachyrella australiensis* (Carter, 1886) (see Table 5). However, the validity of Burton's conclusion was not accepted by van Soest and Rützler (2002) in the Systema Porifera. Therefore, a further examination of the junior synonyms proposed by Burton (1934) was needed and became one of the principal aims that guide this revision. A general review of the historic events about species descriptions and synonyms is provided in Table 5. Emphasis was given to species described based on Indo-Pacific specimens. Remarks were added to clarify the early confusion introduced by Lindgren (1898) when he identified some *Cinachyrella* specimens as *Tetilla ternatensis* (=*Paratetilla bacca*), although his specimens have conspicuos acanthose microxea and lack of calthrop-like spicules, misleading later descriptions for both genera.

*Cinachyrella australiensis* has been recorded from a wide geographic area from the Gulf of Oman (van Soest and Beglinger 2008), Thailand (Kritsanapuntu et al. 2001a-b, Putchakarn 2007), Vietnam (Azzini et al. 2007), Singapore (Lim et al. 2008), North

Australia (McDonald et al. 2002), the Great Barrier Reef in Australia (Burton 1934), Southeast Australia (Carter, 1886), and Indonesia (e.g. Becking et al. 2006, de Voogd and Cleary 2008, de Voogd et al. 2009, Becking et al. 2013), inhabiting coastal mangroves, reefs, and marine lakes.

Ecological studies on the morphological plasticity of *C. australiensis* from North Australia (McDonald et al. 2002) and Thailand (Kritsanapuntu et al. 2001) have concluded that this species can adapt to extreme sedimentation and water current regimes through the variation of the body shape and reinforcement of spicules. Although these surveys showed interesting data on the individual sizes, porocalices, silica/organic content, both of them lack robust taxonomic data (type of spicules and their dimensions). It is therefore unclear whether the observed plasticity can be attributed to natural variation within the same species or may possibly be explained by different species inhabiting different habitats.

**Table 5.** Historic milestones in the taxonomy of *Cinachyrella australiensis* and other *Cinachyrella* species from Indonesia. Asterisk (*) indicates misidentification of *Cinachyrella* specimens as *Paratetilla*.

| Year | Author | Descriptions / Statements |
|---|---|---|
| 1873 | Gray | Description of the monotypic genera *Psetalia* and *Labaria*, with the species *P. globulosa* and *L. hemisphaerica*, respectively. |
| 1886 | Carter | Description of *Tethya cranium* var. *australiensis* from Port Phillip Heads (South Australia) collected at 36 m depth. This species was characterized by the presence of minutely spined (= acanthose) microxea (210 µm). |
| 1888 | Sollas | Establishment of Family Tetillidae. *Tethya cranium* var. *australiensis* was redescribed as *Tetilla* (?) *australiensis*. In addition, Sollas noted that the characteristic microxeas of *T. australiensis* were also present in *T. merguiensis* as well, but were more abundant in *T. australiensis*. |
| 1888 | Lendenfeld | Description of genus *Spiretta* within Family Tetillidae, including two new species *S. raphidiophora* and *S. porosa*, from Port Jackson (SE Australia) and Port Denison (NE Australia), respectively. The former with microxea (240 × 2 µm) and the latter without them. |
| 1891 | Keller | Description of *Cinachyra schulzei* from the Red Sea and Mozambique, with microxea 250 × 5 µm. |
| 1896* | Kieschnick | Description of *Tetilla ternatensis* based on material from Ternate Island (Indonesia). He mentioned "Vierstrahler" (= calthrops). |
| 1898* | Lindgren | Redescription of *Tetilla ternatensis* based on Java material. It is remarkable that he mentioned the presence of numerous microxea (240 × 4 µm) and sigmaspires 24 µm. |
| 1898 | Kieschnick | Description of *Tetilla schulzei* from material of NE Australia to Ambon Island, with microxea (198-220 µm × 4 µm). *T. schulzei* has 'oscula' that we interpret as porocalices. Although Kieschnick entitled *T. schulzei* as new species, it is not clear if he was aware of *Cinachyra schulzei* described by Keller (1891). Three other *Tetilla* species with "Vierstrahler" (= calthrops) spicules were described (see Table 3). |
| 1899 | Thiele | Record of *Tetilla australiensis* from Sulawesi (Indonesia). Specimens with acanthose microxea (180-200 µm × 2.5 µm). |
| 1900* | Thiele | With the redescription of *Tetilla ternatensis* Kieschnick, 1896, Thiele noticed the misidentification of *T. ternatensis* by Lindgren (1898) and pointed out that Lindgren specimens exhibited microxea resembling *Tetilla australiensis* (Carter, 1886). |
| 1900 | Kieschnick | Additional record of *Tetilla schulzei* from Ambon Islands, including description of the specimens, with microxea from 198 to 220 µm × 4 µm. |
| 1900* | Kirkpatrick | Extension of geographical range of *T. bacca* and *T. ternatensis* to Christmas Island. *T. bacca* specimens were described with identical spicules to Lindgren's material from Java. *T. ternatensis* also similar to Lindgren's material of *T. ternatensis,* this is having microxeas and missing calthrops. |
| 1902 | Sollas | Description of *Cinachyra malaccensis* from Malaysia. Cup-shaped porocalices are described together with different spicules, except for microxea. In the available figures, no microxeas are shown. |

| Year | Author | Descriptions / Statements |
|---|---|---|
| 1903* | Thiele | Redescription of *Tetilla ternatensis* Kieschnick, 1898. He drew attention on the misidentification of *T. ternatensis* by Lindgren (1898), clarifying that Lindgren specimens exhibited microxea resembling *Tetilla australiensis* (Carter, 1886). |
| 1903* | Lendenfeld | Designation of a new species *Tetilla lindgreni* based on *T. ternatensis* material described by Lindgren (1898) and Kirkpatrick (1900), excluding the original description of Kieschnick (1896), because the latter one has calthrop-like spicules. Two *Spiretta* species, *S. raphidiophora* and *S. porosa,* transferred to genus *Tetilla*. |
| 1905 | Dendy | Monograph on sponges from Sri Lanka. Description of *Tetilla anomala*, showing remarkable siliceous micro-spherules (4 µm) and no microxeas. Description of *Tetilla poculifera* with smooth microxeas (230 × 5 µm). Description of *Tetilla limicola*, pink-color and root tuft; neither porocalices nor microxea are described. The genus *Paratetilla* was established. |
| 1906 | Baer | Description of *Tethya armata* from Zanzibar (Africa, Indian Ocean). It is characterized by a dermal cortex formed by microxea (166-296 µm × 1-2 µm). |
| 1907 | Lendenfeld | Description of *Cinachyra isis* and *Tethya hebes* from NW Australia, the first one exhibiting smaller microxea (130-160 µm × 2-5.5 µm), and the second one larger rough microxea (= acanthose microxea, 250-275 µm × 4-6 µm). Description of *Cinachyra alba-tridens*, *C. alba-obtusa*, and *C. alba-bidens* species, slightly differentiated by the geometry and abundance of triaenes. He kept the three species because they were collected in three distant localities, Chagos Archipelago, Papua New Guinea, and Tonga Islands, respectively; "alba-group" species do not contain microxeas, and sigmaspires are small (<10 µm). |
| 1911 | Row | Description of *Chrotella ibis* from the Red Sea. Species with smooth microxea (150 × 2.1 µm), sharing this character with *Tetilla poculifera*, and *Paratetilla* species *P. merguiensis*, *P. eccentrica* and *P. cineriformis*. In his description, Row clearly differentiated his species from *T. australiensis* due to the latter having acanthose microxea. |
| 1911 | Hentschel | Description of *Tetilla cinachyroides* from South Australia. Species with acanthose microxea (112-168 µm × 2.5 µm), sigmaspires (10-12 µm) and spherules (5 µm). |
| 1912 | Hentschel | Description of *Cinachyra mertoni* and *Cinachyra nuda* from Aru- and Kei- Islands (Indonesia). Both species contain microxea, the first one smooth 250 µm, whereas in the second one they are acanthose, from 200-280 µm, and no anatriaenes were found. A third species, *Tethya clavigera*, with oscula (similar to porocalices) and no microxea was also described. |
| 1922 | Dendy | Description of *Cinachyra vaccinata* and *C. providentiae* from the Indian Ocean. Both of them with microxea (no mention whether acanthose or not), being 200 × 4 µm in the former, and 220 × 5.5 µm in the latter one. *C. vaccinata* characterized by small hair-like protri- and prodiaenes, terminating in an elongated oval swelling tip unique to this species. *C. providentiae* with bottle-shaped porocalices. |
| 1925 | Wilson | Establishment of *Cinachyrella* as a subgenus of *Tetilla*, with type species *Tetilla hirsuta* Dendy, 1889. The characters used to distinguish *Cinachyrella* species from the other were special depressions (=porocalices) and no specialization of a cortical zone. Wilson included the following species within *Cinachyrella: Cinachyra malaccensis* Sollas, 1902; *Tetilla limicola* Dendy, 1905; *Tetilla anomala* Dendy, 1905; *Cinachyra isis* Lendenfeld, 1907; *C. hamata* Lendenfeld, 1907; *C. alba-tridens* Lendenfeld, 1907; *C. alba-bidens* Lendenfeld, 1907; *C. alba-obtusa* Lendenfeld, 1907; *C. vertex* Lendenfeld, 1907; *Tetilla cinachyroides* Hentschel, 1911; *Cinachyra phacoides* Hentschel, 1911; *Tethya clavigera* Hentschel, 1912; *Cinachyra mertoni* Hentschel, 1912; *Cinachyra nuda* Hentschel, 1912; *Cinachyra vaccinata* Dendy, 1922; *Cinachyra providentiae* Dendy, 1922. In addition, *Cinachyrella crustata* and *Cinachyrella paterifera* were described from Philippines. *C. crustata* with distinctive long and stout promonoenes, no microxea. *C. paterifera* with a characteristic cloaca (= large osculum) on top and root-like structure to attach to sediments, microxea (250 × 2 µm) observed in two specimens although almost absent in the third one of the type series, pointing out a high variability in the presence of microxea within the same individual. |
| 1934 | Burton | Taxonomic revision of *Cinachyra australiensis*. In his compilation, Burton grouped 16 nominal species described in 32 references and designated them as junior synonyms of the widespread species *C. australiensis*. Three different groups were recognized: the *australiensis*-group characterized by the presence of acanthose microxea; the *schulzei*-group with smooth microxea; and the *porosa*-group without microxea. Description of genus *Raphidotethya*. |
| 1954 | de Laubenfels | Identification of *Cinachyra porosa* and *Cinachyra australiensis* from Micronesia (West-Central Pacific). |

| Year | Author | Descriptions / Statements |
|---|---|---|
| 1973 | Thomas | Records of *Cinachyra cavernosa* (Lamarck, 1815) from the Seychelles Islands, having, microxea (126 × 2 µm) sometimes granulated (= acanthose). Among the junior synonyms of *C. cavernosa*, Thomas included *Tethya cranium var. australiensis* Carter, 1886, *Chrotella australiensis* Burton, 1937, and *Chrotella cavernosa* Burton, 1959. However, in the WPD (van Soest et al. 2018) *C. cavernosa* is still a valid species. |
| 1982 | Pulitzer-Finali | Description of *Cinachyra tenuiviolacea* from the Great Barrier Reef (Australia), characterized by a light violet color, small oxeas (up to 2500 µm × 13-25 µm), atrophic anatriaenes, no microxeas, and no protriaenes in the choanosome. |
| 1987 | Rützler | Review of Family Tetillidae, including seven genera (all except for *Fangophilina*). Subgenus *Cinachyrella* was elevated to the hierarchy of genus. |
| 1992 | Rützler and Smith | Review of four species of *Cinachyrella* for the Caribbean region, mainly described by Uliczka (1929). Geometry and size ranges of all spicule types were shown. According to their descriptions, *Cinachyrella kuekenthali* is the most similar species to *C. australiensis*, since both of them have acanthose microxea. |
| 1994 | Hooper and Wiedenmayer | Compilation of *Cinachyra australiensis* synonyms based on Burton (1934) taxonomic decision. |
| 2002 | van Soest and Rützler | Review of the eight genera of tetillids, including *Cinachyrella*. *Cinachyra australiensis* was transferred into the genus *Cinachyrella*. The authors considered that all junior synonyms proposed for *C. australiensis* by Burton (1934) should need further taxonomic revision. Moreover, the genera [*Psetalia*] Gray, 1873 (*nomem oblitum*), [*Labaria*] Gray, 1873 (nomen oblitum) and *Raphidotethya* Burton, 1934 were included as synonyms of the genus *Cinachyrella*. |
| 2018 | van Soest et al. (WPD) | Accepted synonyms of *Cinachyrella australiensis* (Carter, 1886): *Tethya australiensis* Carter, 1886; *Spiretta porosa* Lendenfeld, 1888; *Cinachyra malaccensis* Sollas, 1902; *Tetilla lindgreni* Lendenfeld, 1903; *Tethya armata* Baer, 1906; *Cinachyra isis* Lendenfeld, 1907; *Tetilla cinachyroides* Hentschel, 1911; and *Cinachyra providentiae* Dendy, 1922. Valid *Cinachyrella* spp. from the Indo-pacific (excluding species only found in the Red Sea) comprise 6 species |
| 2018 | This study | From our detailed examination of Indonesian material and type material, we conclude that in Indonesia there are three species: *Cinachyrella australiensis* (Carter, 1886), *Cinachyrella porosa* (Lendenfeld, 1888), and *Cinachyrella paterifera* Wilson, 1922. Further investigations will reveal if the five species from the *C. schulzei*- group can be synonymized or belong to separate and distinctive species. |

***Cinachyrella australiensis* (Carter, 1886)**
Figs 6, 7

*Tethya cranium* var. *australiensis* Carter, 1886: 127 (holotype seen).
*Tetilla*? *australiensis*; Sollas, 1888: 43.
*Spiretta raphidiophora* Lendenfeld, 1888: 43 (type seen).
*Tetilla hirsuta* Dendy, 1889: 75 (type seen).
*Tetilla ternatensis* Lindgren, 1898: 329 pl. 17, fig. 14; pl. 19, Fig. 25 a-e, a', b'. Ternate Not *Tetilla ternatensis*; Kieschnick*, 1896: 527.
*Tetilla australiensis*; Thiele, 1899: 6, pl.1 fig.1; pl. 5, fig.1 a-e. Celebes Sea.
*Tetilla ternatensis*; Kirkpatrick, 1900: 132 (material seen) Not *Tetilla ternatensis* Kieschnick*, 1896: 527.
*Tetilla lindgreni* Lendenfeld, 1903: 18.
*Tetilla australiensis*; Lendenfeld, 1903: 20.
*Tethya hebes* Lendenfeld, 1907: 98, pl. XVI, figs 19–38. 19`South NW Australia, 91 m depth (syntype seen).
*Cinachyra isis* Lendenfeld, 1907: 143, pl. XV, figs 54–58, XVI, figs 1–4. Mermaid Strasse (NW Australia) (syntype seen); Dendy, 1922: 16, pl. 10, figs 3a-b.

*Tetilla cinachyroides* Hentschel, 1911: 281, textfig. 1. NW Australia, Barrow Island.
*Cinachyra nuda* Hentschel, 1912:333, pl. XIII, fig.2; pl. XVIII fig. 13. Aru Island (type seen).
*Cinachyra vaccinata* Dendy, 1922: 14, pl. 1, fig. 4; pl. 11, figs 1a-l. Diego Garcia, Chagos Island (type seen).
*Cinachyra providentiae* Dendy, 1922: 18, pl.1, figs 5–5a; pl. 10, figs2a–f. Providence Island (type seen).
*Tetilla* (*Cinachyrella*) *hirsuta*; Wilson, 1925: 365, pl. 39, fig.4.
*Cinachyra australiensis*; Burton, 1934: 523. In part, not *C. australiensis* in porosa-group, nor *C. australiensis* in schulzei-group; de Laubenfels, 1954: 241, text-fig. 166.
*Cinachyrella anatriaenilla* Fernandez, Kelly, Bell, 2017: 83, figs 2–4.

**Material examined.** Holotype NHMUK 1886.12.15.367, Port Phillip Heads, Southeast Australia (as *Tethya cranium* var. *australiensis*). Holotype NHMUK 1886.8.27.634, Port Jackson, Sidney, Australia (as *Spiretta raphidiophora* Lendenfeld, 1888). NHMUK unreg. type, Gulf of Manaar, Sri Lanka (as *Tetilla hirsuta* Dendy, 1889). NHMUK 1898.12.20.20 Christmas islands (as *Tetilla ternatensis* Kirkpatrick, 1900). Holotype NHMUK 1908.9.24.19–21, 19°17'S 116°E, Gazelle Exp., Western Australia, (as *Tethya hebes* Lendenfeld, 1907). Syntype NHMUK 1908.9.24.74, Mermaid Strait, NW Australia (as *Cinachyra isis* Lendenfeld, 1907). RMNH unreg. fragment taken from the type (pers. comm. NJ de Voogd) and available in Naturalis collections, Aru Island, Indonesia, as *Cinachyra nuda* Hentschel, 1912. Holotype NHMUK 1921.11.7.6, Diego Garcia, Chagos Islands (as *Cinachyra vaccinata* Dendy, 1922). Holotype NHMUK 1921.11.7.8, Providence Island, Seychelles (as *Cinachyra providentiae* Dendy, 1922). **INDONESIA**. East Kalimantan, *Berau reef,* RMNH.POR.11101, RMNH.POR.11102, RMNH.POR.11103, RMNH.POR.11104, RMNH.POR.11105, RMNH.POR.11106, RMNH.POR.11107, RMNH.POR.11108, RMNH.POR.11109, RMNH.POR.11110, RMNH.POR.11111, RMNH.POR11112, RMNH.POR.11113, RMNH.POR.11114, RMNH.POR.11115, RMNH.POR.11116, RMNH.POR.11117, RMNH.POR.11210, RMNH.POR.11124, RMNH.POR.11125, RMNH.POR.11126, RMNH.POR.11127, RMNH.POR.11128, RMNH.POR.11129, RMNH.POR.11130, RMNH.POR.11118, RMNH.POR.11119, RMNH.POR.11120, RMNH.POR.11121, RMNH.POR.11122, RMNH.POR.11123; RMNH.POR.11132; RMNH.POR.11133, RMNH.POR.11134, RMNH.POR.11135, RMNH.POR.11136; *Pea Bay,* RMNH.POR.11162; *Haji Buang Lake,* RMNH.POR.11137, RMNH.POR.3511, RMNH.POR.3512, RMNH.POR.3513, RMNH.POR.3516, RMNH.POR.3517; *Kakaban Lake,* RMNH.*POR.*11161, RMNH.POR.11138, RMNH.POR.11139, RMNH.POR.11140, RMNH.POR.11141, RMNH.POR.11142, RMNH.POR.11143, RMNH.POR.11144, RMNH.POR.11145, RMNH.POR.11146, RMNH.POR.11147, RMNH.POR.11148, RMNH.POR.11149, RMNH.POR.11150, RMNH.POR.11151, RMNH.POR.11152, RMNH.POR.11153, RMNH.POR.11154, RMNH.POR.11155, RMNH.POR.11156, RMNH.POR.11157, RMNH.POR.11158, RMNH.POR.11159, RMNH.POR.11160. Java, *Thousand*

*Islands,* RMNH.POR.1969. Ternate, *Ternate reef,* RMNH.POR.11308. Sulawesi, *Bunaken,* RMNH.POR.3108, RMNH.POR.3112, RMNH.POR.3119, RMNH.POR.3122. West Papua, *Sawaundarek Lake,* RMNH.POR.11163, RMNH.POR.11164, RMNH.POR.11165, RMNH.POR.11166, RMNH.POR.11167; *Gam Island, Wallace Lake,* RMNH.POR.11168, RMNH.POR.11169 *Outside Wallace Lake,* RMNH.POR.11170, RMNH.POR.11171, RMNH.POR.11172, RMNH.POR.11173; *Gam Island, Blue Water Mangrove,* RMNH.POR.11174, RMNH.POR.11175, RMNH.POR.11176, RMNH.POR.11177, RMNH.POR.11178, RMNH.POR.11179, RMNH.POR.11180, RMNH.POR.11181, RMNH.POR.11182, RMNH.POR.11183, RMNH.POR.11184, RMNH.POR.11185, RMNH.POR.11186, RMNH.POR.11187, RMNH.POR.11188, RMNH.POR.11189, RMNH.POR.11190, RMNH.POR.11191, RMNH.POR.11192; *Ctenophore Lake,* RMNH.POR.11193, RMNH.POR.11194, RMNH.POR.11195, RMNH.POR.11196, RMNH.POR.11197; *Outside Ctenophore Lake,* RMNH.POR.11198, RMNH.POR.11199, RMNH.POR.11200, RMNH.POR.11201; *Big Caulerpa Lake,* RMNH.POR.11202, RMNH.POR.11203; *Outside Big Caulerpa lake,* RMNH.POR.11204; *Gam Island,* RMNH.POR.11205, RMNH.POR.11206.

**Other material**: Singapore, RMNH.POR.3520, RMNH.POR.2440, RMNH.POR. 2505.

**Other types and material examined (not included as synonyms of *C. australiensis*):** NHMUK 1892.8.8.8. Macclesfield Bank, South China Sea *Cinachyra schulzei* (unpublished material). Holotype NHMUK 1908.9.24.75 Red Sea, *Cinachyra trochiformis* Keller, 1891. Holotype NHMUK 1907.2.1.14, Gulf of Manaar, Sri Lanka, *Tetilla poculifera* Dendy, 1905. Holotype NHMUK 1912.2.1.35, Tella Tella Kebira, Red Sea, *Chrotella ibis* Row, 1911. RMNH unreg. fragment taken from the type (pers. comm. NJ de Voogd) available in Naturalis collections, Kei Island, Indonesia, *Cinachyra mertoni* Hentschel, 1912.

**Description. External morphology.** Globular sponges, size from 4 to 10 cm in diameter (Figure 6A, B). Surface hispid due to the projecting spicules; covered by numerous porocalices. Porocalices are abundant bowl-shape with open oval apertures, up to 10 × 5 mm and 5 mm deep, or bottle-shape, up to 18 × 6.5 mm, with minuscule apertures (2–3 mm diameter), size of porocalices can vary between habitats; a cloaca, defined as a central exhalant cavity (Boury-Esnault and Rützler, 1997), is distinguishable at the top of some specimens (Figure 6A); in preserved material some porocalices are open. Color generally bright yellow when alive, which turns paler or even white in ethanol. In the field, the sponge can appear brownish due to sediment or greenish due to association with algae.

**Skeleton.** No cortex. Skeleton composed by bundles of oxeas and triaenes radiating from a central core.

**Megascleres.** Holotype and Indonesian specimens' measurements are shown in Table 6. Holotype, oxeas 3375–4135.5–5500 µm × 15–24.7–37.5 µm (Figure 6D, K); no triaenes were observed in the type specimen; in Carter's description, protriaenes are described (135 µm long) and the absence of anatriaenes was explained as their heads

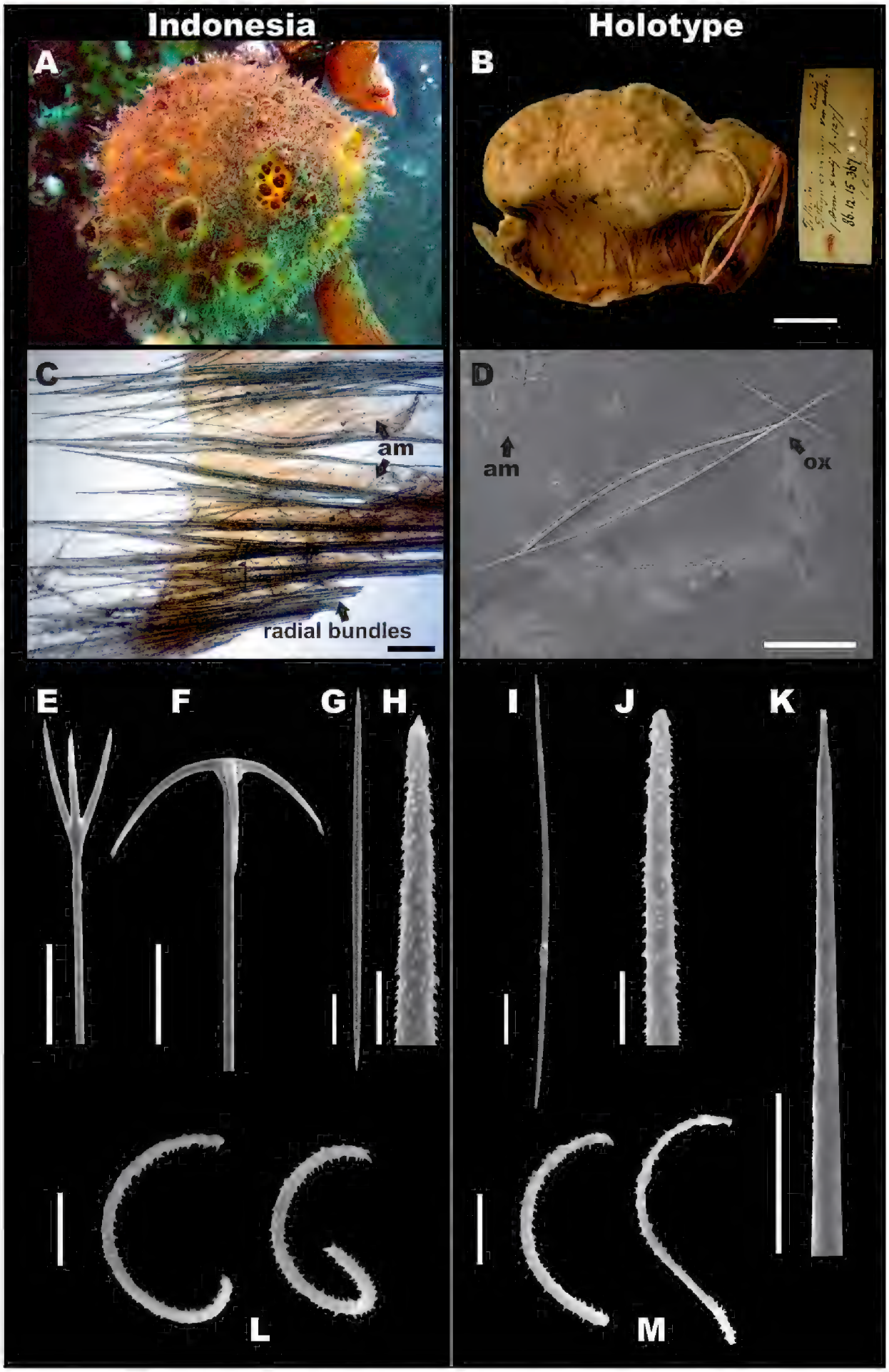


**Figure 6.** *Cinachyrella australiensis*. **A, C, E-H, L** RMNH.POR.11139, Kakaban lake, Indonesia (left side) **B, D, I-K, M** holotype NHMUK 1886.12.15.367, Port Phillip Heads, Australia (right side) **A** In situ photograph showing porocalices **B** dry specimen, lateral view **C** skeleton showing acanthose microxeas (*am*) and radial bundles with oxeas **D** spicule montage showing acanthose microxeas (*am*), and oxeas (*ox*) **E** protriaene **F** anatriaene **G** Acanthose microxea, full lenght **H** acanthose microxea, detail **I** acanthose microxea, full length **J** acanthose microxea, detail **K** oxea, end detail **L, M** sigmaspires. Scale bars: 1 cm(**B**); 500 µm (**C, D**); 20 µm (**E–G, I**); 5 µm (**H, J, L, M**); 50 µm (**K**).

**Table 6.** Spicule measurements of eight specimens *Cinachyrella australiensis*, five specimens of *C. anomala*, four specimens of *C. paterifera* from different regions (n = 10 per spicule type and dimension with minimum-**mean**-maximum). Asterisk (*) indicate that rhabd of spicules were broken and no measurement was possible. Double asterisk (**) indicate that a particular spicule type was not observed.

| Measurements | | *Cinachyrella australiensis* | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | NHMUK86.12.15.367 (Holotype) | RMNH. POR.11120 | RMNH. POR.11146 | RMNH. POR.11123 | RMNH. POR.11139 | RMNH. POR.11118 | RMNH. POR.11308 | RMNH. POR.11192 |
| Locality | | Port Phillip Heads | Berau | Kakaban | Berau | Kakaban | Berau | Ternate | Raja Ampat |
| Habitat | | Reef? | Reef | Marine Lake | Reef | Marine Lake | Reef | Reef | Mangrove |
| Oxeas | Length | 3375–**4135.5**–5500 | 1000–**3332**–4500 | 1375–**2912**–4000 | 2425–**3822.8**–5500 | 2250–**3066**–4250 | 2300–**4315**–5750 | 1500–**2676**–3800 | 2000–**2658.3**–3750 |
| | Width | 15–**24.7**–37.5 | 10–**40**–52.5 | 17.5–**33.9**–55 | 25–**41.7**–60 | 17.5–**26.4**–35 | 37.5–**59.1**–77.5 | 12.5–**30.3**–60 | 25–**31.3**–37.5 |
| Anatriaene | Rhabd | ** | 2750–**3271.**9–3650 | 2250–**3317.**9–4250 | 2700–**3083.**3–3300 | * | * | * | * |
| | Rhabd width | | 5–6–7.5 | 2.5–**5.3**–7.5 | 4–**4.9**–5 | 5–**5**–5 | 5–**5**–5 | 7.5–**8.4**–10 | 5–**5.3**–7.5 |
| | Cladi total | | 50–**63.5**–85 | 30–**74.2**–100 | 45–**58**–70 | 40–**55**–70 | 60–**81**–100 | 55–**79.4**–100 | 70–**83**–100 |
| | Cladi length | | 40–**49.5**–65 | 20–**60.4**–80 | 30–**42.5**–50 | 35–**45**–60 | 32.5–**49.5**–57.5 | 30–**49.1**–67.5 | 50–**66**–80 |
| | Cladi width | | 2.5–**4.5**–5 | 2.5–**3.5**–5 | 4–**5.6**–10 | 5–**5**–5 | 5–**5.1**–6 | 5–**5.6**–7.5 | 5–**5**–5 |
| Protriaene | Rhabd length | ** | 3900–**4550**–5800 | 3700–**4262.**5–4750 | 840–**3522.**5–5000 | 2250–**2375**–2500 | ** | * | * |
| | Rhabd width | | 10–**13.3**–20 | 12.5–**14.7**–15 | 10–**12.5**–15 | 2.5–**5.9**–7.5 | | 7.5–**8.3**–10 | 2.5–**5**–7.5 |
| | Cladi total | | 20–**46.9**–70 | 20–**58.8**–80 | 40–**60.8**–80 | 40–**55**–80 | | 45–**50.4**–55 | 25–**70.5**–100 |
| | Cladi length | | 35–**66.3**–110 | 25–**93.8**–170 | 75–**95.8**–130 | 50–**79.5**–110 | | 40–**77.9**–120 | 30–**108**–150 |
| | Cladi width | | 5–**7.9**–10 | 10–**11.6**–12.5 | 10–**10.8**–12.5 | 2.5–**4.8**–5 | | 5–**5.8**–7.5 | 2.5–**4.**3–5 |
| Strongyle | Length | ** | — | 4000–**4000**–4000 | 2450–**3041.7**–4200 | | | 2200–**2650**–2850 | |
| | Width | | | 50–**50**–50 | 35–**43.3**–60 | | | 32.5–**39.4**–50 | |
| Acanthose microxea | | 117–**166.9**–260 | 160–**197.3**–230 | 150–**165**–200 | 200–**230**–270 | 150–**183.5**–240 | 157.5–**189.5**–225 | 170–**191.4**–225 | 137.5–**154**–175 |
| Sigmaspires | | 10–**14.**4–17.5 | 12.5–**1**5–17.5 | 10–**12.**3–15 | 12.5–**14.8**–17.5 | 10–**12**–15 | 15–**16.5**–20 | 12.5–**15.7**–20 | 12.5–**14.8**–17.5 |

**Table 6.** Continued.

| Measurements | | *Cinachyrella porosa* | | | | | *Cinachyrella paterifera* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | NHMUK86.8.27.632–3 (Holotype) | RMNH. POR.11226 | RMNH. POR.11244 | RMNH. POR.11262 | RMNH. POR.11309 | USNM21314 (Holotype) | RMNH. POR.11207 | RMNH. POR.11213 | RMNH. POR.11208 |
| **Locality** | | Port Denison | Tanah Banban | Teluk Pea | Raja Ampat | Ternate | Philippines | Berau | Raja Ampat | Berau |
| **Habitat** | | Reef | Marine Lake | Reef | Reef | Reef | Reef | Reef | Reef | Reef |
| **Oxeas** | Length | 820–**2553.2**–3750 | 550–**2138.1**–3750 | 1350–**2702.5**–4000 | 1250–**2304.2**–3150 | 1500–**2710**–3500 | 1400–**3011.5**–4750 | 2850–**3580.6**–4500 | 1850–**3060**–5000 | 800–**2748.2**–4500 |
| | Width | 7.5–**29.4**–47.5 | 5–**28.2**–60 | 7.5–**29.5**–47.5 | 12.5–**29.4**–40 | 7.5–**32.6**–45 | 10–**34.5**–62.5 | 30–**46.1**–62.5 | 12.5–**35.6**–55 | 5–**34.2**–75 |
| **Anatriaene** | Rhabd | * | * | * | * | * | * | * | * | 4250–**4250**–4250 |
| | Rhabd width | 2.5–**5.8**–7.5 | 10–**12**–15 | 5–**7.8**–10 | 5–**5**–5 | 5–**6.1**–7.5 | 5–**7.5**–10 | 5–**6.6**–10 | 7.5–**8.8**–10 | 5–**5**–5 |
| | Cladi total | 50–**67.6**–100 | 65–**71**–80 | 60–**65**–70 | 50–**62.9**–70 | 50–**62.5**–75 | 17.5–**24.2**–30 | 17.5–**37.5**–75 | 70–**90**–110 | 65–**79.3**–110 |
| | Cladi length | 30–**42**–60 | 45–**56**–65 | 40–**52**–70 | 40–**51.4**–60 | 30–**50.4**–62.5 | 2–**6.5**–10 | 7.5–**25.7**–80 | 50–**65**–80 | 42.5–**58.2**–90 |
| | Cladi width | 2.5–**5.6**–7.5 | 10–**10.5**–12.5 | 2.5–**6.6**–7.5 | 2.5–**4.6**–5 | 5–**5.4**–7.5 | 5–**5.8**–7.5 | 5–**6.4**–10 | 7.5–**7.5**–7.5 | 2.5–**4.3**–5 |
| **Protriaene** | Rhabd length | * | * | * | * | * | * | 3500–**4210**–5350 | * | 4300–**4689.3**–5100 |
| | Rhabd width | 5–**7.3**–12.5 | 5–**8.8**–15 | 2.5–**6.5**–10 | 2.5–**3.6**–5 | 2.5–**5**–7.5 | 10–**10**–10 | 5–**9.5**–12.5 | 5–**7.8**–10 | 10–**15.2**–17.5 |
| | Cladi total | 25–**44.4**–65 | 20–**51.25**–80 | 40–**59**–80 | 30–**44.3**–60 | 50–**53.8**–67.5 | 30–**32.5**–35 | 35–**53.9**–75 | 40–**70**–100 | 30–**37.3**–60 |
| | Cladi length | 35–**73**–110 | 30–**77.5**–125 | 60–**100**–160 | 40–**67.1**–100 | 50–**78.3**–137.5 | 22.5–**31.3**–40 | 20–**74.1**–130 | 30–**82.5**–140 | 40–**51.6**–80 |
| | Cladi width | 5–**5.1**–7.5 | 5–**7.5**–15 | 2.5–**5.5**–10 | 2.5–**2.5**–2.5 | 2.5–**4**–5 | 7.5–**7.5**–7.5 | 2.5–**6.8**–7.5 | 5–**6.6**–7.5 | 10–**11.6**–15 |
| **Strongyle** | Length | 2650–**2650**–2650 | ** | 3350–**3350**–3350 | ** | ** | * | 2450–**2800**–3250 | 2100–**2975**–3700 | 1800–**1862.5**–1925 |
| | Width | 35–**35**–35 | | 45–**45**–45 | | | 45–**45**–45 | 40–**43.1**–50 | 35–**45.3**–62.5 | 35–**37.5**–40 |
| **Acanthose microxea** | | | | | | | | | | |
| **Sigmaspires** | | 5–**8**.6–12.5 | 7.5–**8**.5–10 | 5–**8.9**–12.5 | 5–**8**–10 | 5–**8**–10 | 10–**13.2**–17.5 | 12.5–**15.3**–17.5 | 12.5–**14.5**–17.5 | 12.5–**16.2**–20 |
| **Protriaene (hair–like)** | Rhabd length | | | | | | * | * | * | 550–**698.**9–820 |
| | Width | | | | | | 2.5–**2.**5–2.5 | 2.5–**2.5**–2.5 | 2.5–**2.5**–2.5 | 2–**2.2**–2.5 |
| | Cladi total | | | | | | 7.5–**12.5**–17.5 | 7.5–**10.9**–17.5 | 12.5–**13.6**–15 | 7.5–**11.7**–20 |
| | Cladi length | | | | | | 12–**15.5**–20 | 17.5–**21.6**–25 | 12–**14.5**–17.5 | 10–**14.4**–25 |
| | Cladi width | | | | | | 2.5–**2.5**–2.5 | 2–**2.1**–2.5 | 2.5–**2.5**–2.5 | 1–**1.7**–2.5 |

broke off when collected; Indonesian specimens have a wide size range of oxea 1000–5500 μm (Figure 6C), abundant anatriaenes (Figure 6F), with rhabd 2250–3224.4–4250 μm × 2.5–5.7–10 μm, cladi thin, mainly with obtuse angles 30–70.6–100 μm × 20–51.7–80 μm × 2.5–4.9–10 μm; protriaenes (Figure 6E), with thin and long cladi (20–57.1–80 μm × 25–86.9–170 μm × 2.5–7.5–12.5 μm), rhabd up to 5800 × 20 μm, tapering to dimensions of < 1 μm; few prodiaenes also observed, having smaller cladi (20–30 μm × 20–30 μm); no calthrop-like triaenes.

**Microscleres.** Numerous acanthose microxeas, holotype, 117–166.9–260 μm (Figure 6I, J), slightly larger in the Indonesian material 137.5–184.7–270 μm (Figure 6G, H); sigmaspires vary within the same range in both, holotype and Indonesian specimens, 10–14.4–20 μm, C-S shape (Figure 6L, M).

**Ecology.** *Cinachyrella australiensis* occurs in reefs, mangroves, and marine lakes, ranging in depths from 0 to at least 30 m, possibly deeper. Specimens can be covered by sand and mud; or in symbiosis with algae, resulting in green external color. This species produces 1–2 mm sized buds (Figure 8) and buds are extensively observed in specimens collected from marine lake habitats.

**Distribution.** *Cinachyrella australiensis* has a wide distribution in Indonesia, including Berau, Bunaken, Raja Ampat, Ternate, and Java. Previous Indonesian records are from Spermonde Archipelago in Sulawesi (de Voogd and Cleary 2005, Becking et al. 2006, de Voogd et al. 2006), North Sulawesi (Calcinai et al. 2017), Berau (de Voogd et al. 2009, Becking et al. 2013), Thousand Islands in Java (de Voogd and Cleary 2008), and Raja Ampat (Becking 2008). In addition, this species has also been found in Gulf of Oman (van Soest and Beglinger 2008), Seychelles Islands (Thomas 1973) Southwest Madagascar (Vacelet et al. 1976), Zanzibar (Pulitzer-Finali 1993), Thailand (Kritsanapuntu et al. 2001a-b, Putchakarn 2007), Singapore (Lim et al. 2008), Vietnam (Azzini et al. 2007), Philippines (Longakit et al. 2005), Northern Territory of Australia (McDonald et al. 2002), and the Great Barrier Reef in Australia (Burton 1934).

**Remarks.** In the type description of *C. australiensis* Carter (1886), the author did not observe anatriaenes as it can be interpreted from his statement: "I saw no anchors (smaller tetractinellids with recurved arms); but as their heads when exposed are generally broken off (for they catch in everything that they touch), it does not follow that they do not form part of the spiculation, particularly as they are present in most of the other species that I have been described (sic)". We examined the holotype kept at the Natural History Museum (NHMUK 1886.12.15.367) and found neither anatriaenes nor protriaenes. In addition, most of the oxeas were broken in the type specimen. Within all the examined material there is a high variability in the presence or absence of triaenes without a distinct geographic pattern. This variation may be related to where the sponge was cut, as it seems that triaenes are particularly abundant around the porocalices compared to other parts of the sponge. These fragile spicules are also easily broken off. We still assign our specimens to the species *C. australiensis* due to the characteristic presence of acanthose microscleres. It is furthermore one of the most common names used in the literature since its description and without further evidence we do not want to cause more confusion. Further examination of *Cinachyrella* specimens from Australia, in particular from the type locality of *C. australiensis*, will

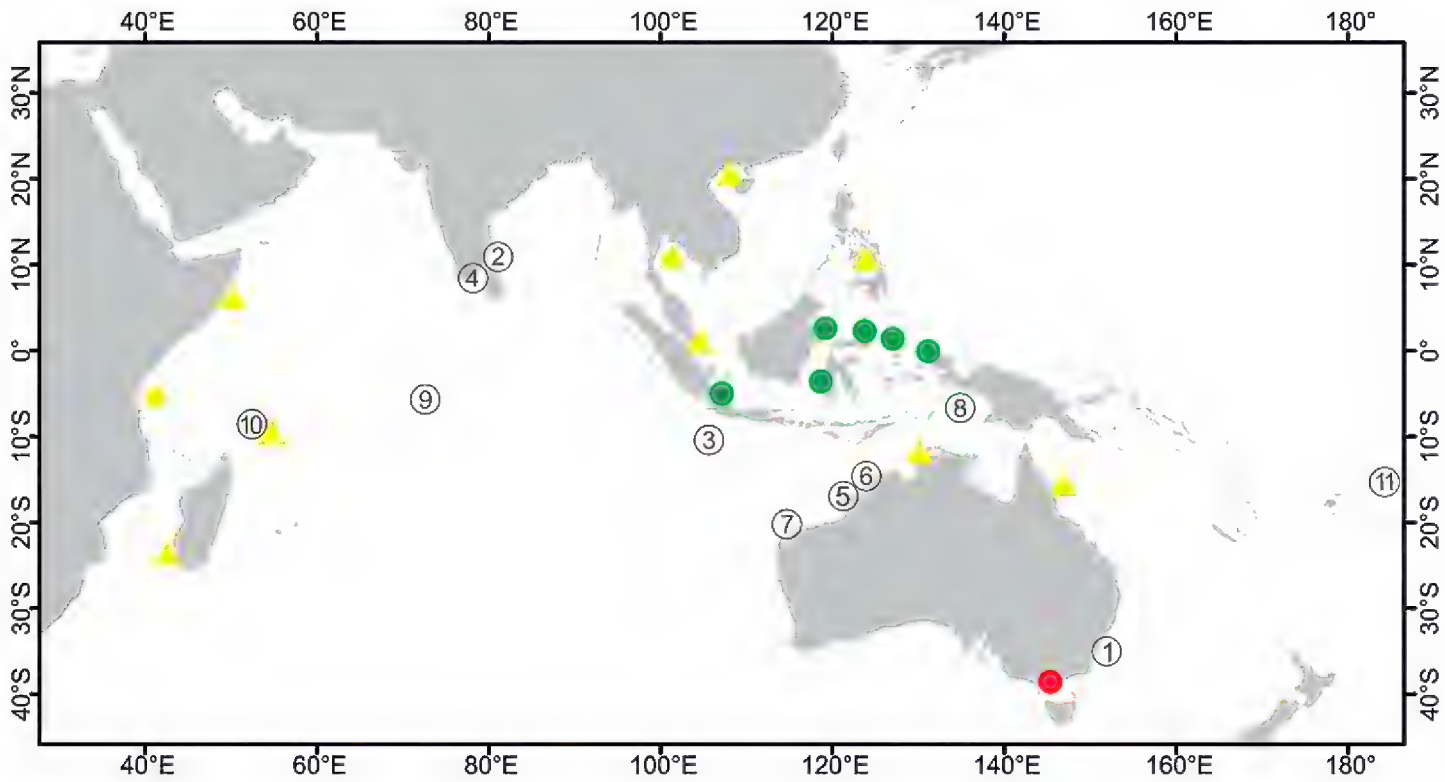


**Figure 7.** Distribution of *Cinachyrella australiensis*. Red dot: type locality, *Tethya cranium* var. *australiensis* Carter, 1886, Port Phillip Heads, Southeast Australia. Green dots: Indonesian localities where the species was collected recently. Yellow triangles: Non-Indonesian localities, Seychelles Islands, Southwest Madagascar, Zanzibar, Thailand, Singapore, Vietnam, Philippines, Northern Territory of Australia, and the Great Barrier Reef in Australia. Circled numbers: type localities of synonymized species **1** *Spiretta raphidiophora* Lendenfeld, 1888, Port Jackson, Sidney, Australia **2** *Tetilla hirsuta* Dendy, 1889, Gulf of Manaar, Sri Lanka **3** *Tetilla lindgreni* Lendenfeld, 1903, Christmas Island **4** *Tetilla poculifera* Dendy, 1905, Gulf of Manaar, Sri Lanka **5** *Tethya hebes*, 1907, at 19° South on the NW coast of Australia **6** *Cinachyra isis* Lendenfeld, 1907, Mermaid Strait, NW Australia **7** *Tetilla cinachyroides* Hentschel, 1911, Barrow Island, NW Australia **8** *Cinachyra nuda* Hentschel, 1912, Aru Island, Indonesia **9** *Cinachyra vaccinata* Dendy, 1922, Diego Garcia, Chagos Islands **10** *Cinachyra providentiae* Dendy, 1922, Providence Island, Seychelles **11** *Cinachyrella anatriaenilla* Fernandez, Kelly, Bell, 2017, American Samoa.

shed more light in this situation. It is quite possible that after a review of specimens from Southern Australia, it will be evident that the Indonesian specimens that we assign to *C. australiensis* should in fact be assigned to another species. In that case one of the junior synonyms should be used, e.g. *C. raphidiophora* or *C. hirsuta.*

Although our focus was on Indonesian species, it was unavoidable to attempt, for the first time after Burton's review (1934), check the status of his large list of junior synonyms, because some of them were described or later found in Indonesian localities. We gathered as many type specimens as possible, most of them repositories of the NHMUK (London) and NMNH (Washington DC). The main criteria we used to suggest a species as junior synonym of *C. australiensis* were the presence of acanthose microxea and that the mega- and micro-scleres have the same size range of the species. Therefore, here we include as junior synonyms the following species from Burton's list: *Spiretta raphidiophora* Lendenfeld, 1888; *Tetilla hirsuta* Dendy, 1889; *Cinachyra isis* Lenfenfeld, 1907; *Tetilla cinachyroides* Hentschel, 1911; *Cinachyra nuda* Hentschel, 1912; *Cinachyra vaccinata* Dendy, 1922; *Cinachyra providentiae* Dendy, 1922. They all fulfill the *C. australiensis* description.

**Here we provide further remarks on the following species, in chronologic order:**

*Tetilla lindgreni* Lendenfeld, 1903 was described as a new species to separate it from *T. ternatensis* Kieschnick, 1896, as *T. ternatensis*is is a *Paratetilla* based on the presence of calthrop-like spicules. Lendenfeld noticed that both, Lindgren's (1898) and subsequently Kirkpatrick's (1900) material, lack such calthrop-like spicules, and instead, they have acanthose microxea similar to other *Tetilla* specimens described in his monograph (Lendenfeld 1903). From that material, we checked Kirkpatrick's specimens and suggest that *T. lindgreni* is a junior synonym of *C. australiensis*.

*Tethya hebes* Lendenfeld, 1907 has acanthose microxea and it has most of *C. australiensis* characters, yet it was excluded from Lendenfeld's Cinachyrinae-group (with porocalices) because he did not observe porocalices. The type specimens of *T. hebes* examined at the NHM (NHMUK 1908.9.24.66) are two small fragments, about 1.2 × 1 cm, and it is not possible to observe neither discard the presence of porocalices. Apart from that, the general skeletal arrangement and spicule configuration suggest that *T. hebes* fulfil all other morphological characteristics of *C. australiensis*. Therefore, we suggest that *T. hebes* is a junior synonym of *C. australiensis*.

We exclude from *C. australiensis* some junior synonyms that are part of the *schulzei*-group species proposed by Burton (1934). These species have smooth microxea and include Keller's (1891) species from the Red Sea, *Cinachyra schulzei* and *Cinachyra trochiformis*. The taxonomic case of *C. schulzei* becomes more complicated as Kieschnick (1898, 1900) described a new species named *Tetilla schulzei* from material collected in Amboine islands of Indonesia with porocalices and spicules diagnostic of *Cinachyrella*, including microxea. However, Kieschnick did not mention any observation whether or not the microxea of *T. schulzei* have acanthose surface. The set of characters of *Cinachyra schulzei* Keller, 1891 and *Tetilla schulzei* Kieschnick, 1898 correspond to *Cinachyrella*. However, we consider that both species should be treated as homonyms because they were described under two different genera, from different and distant localities and we were not able to find their type material to verify if they could be synonymized. Other species within the *schulzei*-group are *Cinachyra mertoni* Hentschel, 1912 from Kei island in Indonesia; *Tetilla poculifera* Dendy, 1905 from Sri Lanka; and *Chrotella ibis* Row, 1911 from the Red Sea. Special attention and a further revision is proposed for the *schulzei*-group of species, as we did not observe any specimen of the genus *Cinachyrella* with smooth microxea within the Indonesian material examined in this study. It is important to mention that thin smooth microxea were observed in both *Paratetilla* species, *P. bacca* and *P. arcifera*, but they also have calthrops as a diagnostic character of the genus.

We also exclude from *C. australiensis* two of the junior synonyms still present in the WPD (van Soest et al. 2018). First, *Tethya armata* Baer, 1906, because it is clear from the description that this species has a proteinous cortex reinforced by microxeas, resembling other *Craniella* species. Second, we exclude the junior synonym *Cinachyra malaccensis* Sollas, 1902, as the description does not mention the presence of microxea, therefore we suggest to synonymise it with *C. porosa.*

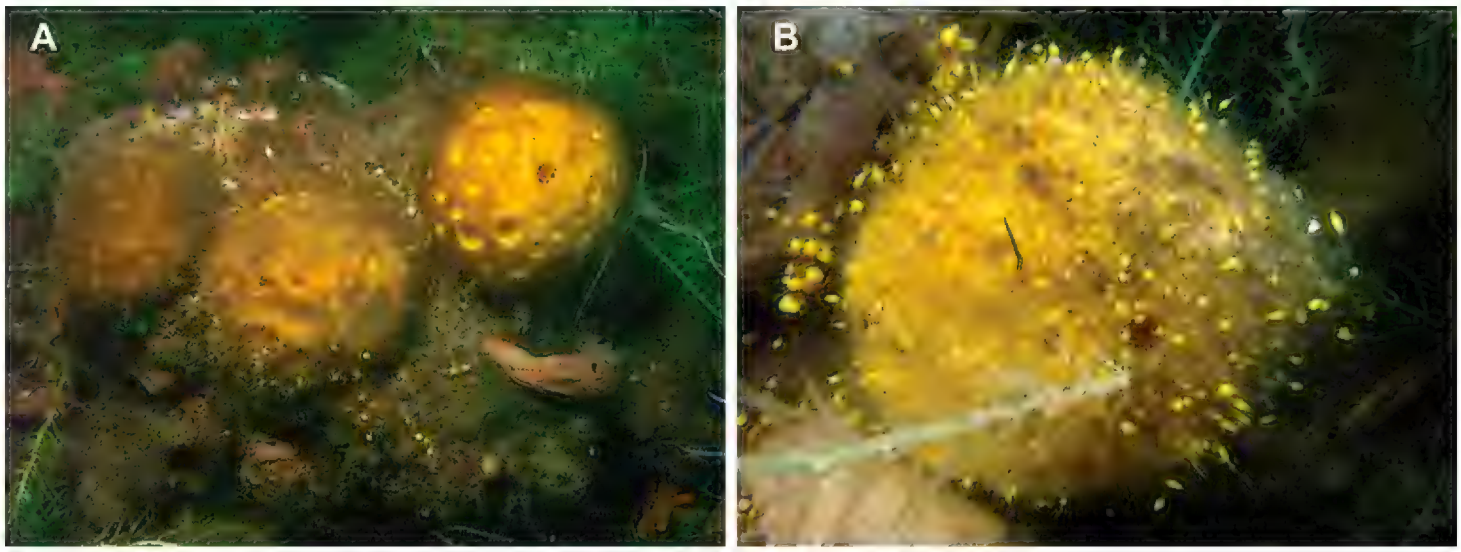


**Figure 8.** Budding and sediment capture of *Cinachyrella* species **A** Three individuals of *C. porosa* in Haji Buang lake, East Kalimantan, Indonesia, showing distribution of buds beyond the individuals and sediment capture **B** Close up of *C. porosa* with detail of buds. Each individual is approximately 4 cm in diameter.

In our view, the recently erected species of *Cinachyrella anatriaenilla* is junior synonym of *C. australiensis,* because the oxea and the microscleres fall within the size range of the type species of *C. australiensis* as well as the specimens we have included in this review. The authors distinguish their species from *C. australiensis* on the basis of having only one category of oxeas versus two categories in *C. anatriaenilla*. However, we do not recognize size classes in oxea in any of the *Cinachyrella* specimens and types, but rather a continuos range in size (1000–5500 µm for *C. australiensis*). The oxea of *C. anatriaenilla* fall within the size range of the type specimen of *C. australiensis* as well as the other reviewed material of *C. australiensis*. In addition, the authors based their statements on the revision of the type specimen of *C. kuekenthali*, which is from the west Atlantic, but they did not review the type specimen of *C. australiensis* nor any of the other species with acanthose microxea from the Indo-Pacific.

Recent molecular studies (Szitenberg et al. 2013, Schuster et al. 2017) show that *Cinachyrella* is a polyphyletic genus. It is beyond the scope of the current study to review the taxonomic status of the genus *Cinachyrella*. Within *C. australiensis* there are different genotypes (Schuster et al. 2017) that possibly represent morphologically cryptic species. Among the high morphological variation observed within our Indonesian specimens, some trends could be highlighted among the different populations. For instance, specimens from reefs of Berau were generally larger (up to 8 cm in diameter) and their porocalices had a bottle-shape with a small aperture (1 to 4 mm) and the cavity was often occupied by a shrimp. Although these characteristics resemble *C. providentiae*, the latter is one of the junior synonyms that we propose for *C. australiensis* based on spicule dimensions and forms. Specimens from Raja Ampat generally had smaller acanthose microxeas (Table 6), while in some specimens collected in marine lakes few abnormal spicules were observed. Yet, in all cases we could not detect consistent, quantifiable morphological differences.

***Cinachyrella porosa* (Lendenfeld, 1888)**
Figs 9, 10

*Spiretta porosa* Lendenfeld, 1888: 43 (type seen).
*Cinachyra malaccensis* Sollas, 1902: 219, pl. XIV, fig. 2; pl. XV, fig. 5. Malacca Strait.
*Tetilla porosa*; Lendenfeld, 1903: 22.
*Tetilla anomala* Dendy, 1905: 91, pl. III, fig.5 (type seen).
*Cinachyra albatridens* Lendenfeld, 1907: 149, pl. XV, figs 7–9 (type seen).
*Cinachyra albaobtusa* Lendenfeld, 1907: 154, pl. XVI, figs 45–52 (type seen).
*Cinachyra albabidens* Lendenfeld, 1907: 151, pl. XVI, figs 39–44 (type seen).
*Tethya clavigera* Hentschel, 1912: 327, pl. XVI, fig.1, pl. XVIII, fig. 10 In Aru Island, Beach Ngaiboor Trangan.
*Cinachyra anomala*; Dendy, 1922: 20, pl. 1, fig. 3 (material seen).
*Cinachyra porosa*; de Laubenfels, 1954: 240, pl. XI, fig. b (material seen).

**Material examined.** Holotype NHMUK 1886.8.29.632-633, Port Denison, Australia (as *Spiretta porosa*). NHMUK 1907.2.1.12, Chilaw, Sri Lanka (as *Tetilla anomala*). NHMUK 1908.2.9.40-42, Diego Garcia, Chagos Archipelago (as *Cinachyra albatridens*). NHMUK 1908.9.24.72, Anachoreten (=Keniet) Islands, Papua New Guinea (as *Cinachyra albaobtusa*). NHMUK 1908.9.24.71, Tonga Islands (as *Cinachyra albabidens*). **INDONESIA**, East Kalimantan, *Berau reef,* RMNH. POR.11228 [LT628324]; *Pea Bay,* RMNH.POR.11242, RMNH.POR.11243, RMNH.POR.11244 [JX177888]; *Bamban Lake,* RMNH.POR.11222, RMNH. POR.11223, RMNH.POR.11224, RMNH.POR.11225 [LT628327], RMNH. POR.11226; RMNH.POR.11226; *Bandong Lake,* RMNH.POR.11227; *Haji Buang Lake,* RMNH.POR.11236, RMNH.POR.11237, RMNH.POR.11238, RMNH. POR.11239, RMNH.POR.11240 [LT628325], RMNH.POR.11230, RMNH. POR.11231, RMNH.POR.11232 [LT628326], RMNH.POR.11233, RMNH. POR.11234, RMNH.POR.11235, RMNH.POR. 3514; *Kakaban Lake,* RMNH. POR.11241. Java, *Thousand Islands,* RMNH.POR.1998, RMNH.POR.2108. Sulawesi, *Bunaken,* RMNH.POR.3105. Ternate, *Ternate reef,* RMNH.POR.11309. West Papua, *Sawaundarek Lake,* RMNH.POR.11245 [JX177884], RMNH. POR.11246 [LT628323], RMNH.POR.11247, RMNH.POR.11248; *Ctenophore Lake,* RMNH.POR.11249, RMNH.POR.11250, RMNH.POR.11251, RMNH. POR.11251, RMNH.POR.11252, RMNH.POR.11253, RMNH.POR.11254, RMNH.POR.11255, RMNH.POR.11256, RMNH.POR.11257, RMNH. POR.11258, RMNH.POR.11259; *Outside Ctenophore Lake,* RMNH.POR.11260, RMNH.POR.11261, RMNH.POR.11262; *Gam Island, Reef flat,* RMNH. POR.11263; *Gam Island, Mangrove,* RMNH.POR.11264.

**Description. External morphology.** Globular sponges, size from 3 to 5 cm in diameter (Figs 9A, 10A, B). Surface highly hispid due to the projecting spicules, covered by numerous porocalices. Porocalices are bowl-shape, with rounded apertures, up to 4 × 5 mm and 5 mm deep, abundant; no cloaca; in preserved material some porocalices are closed.

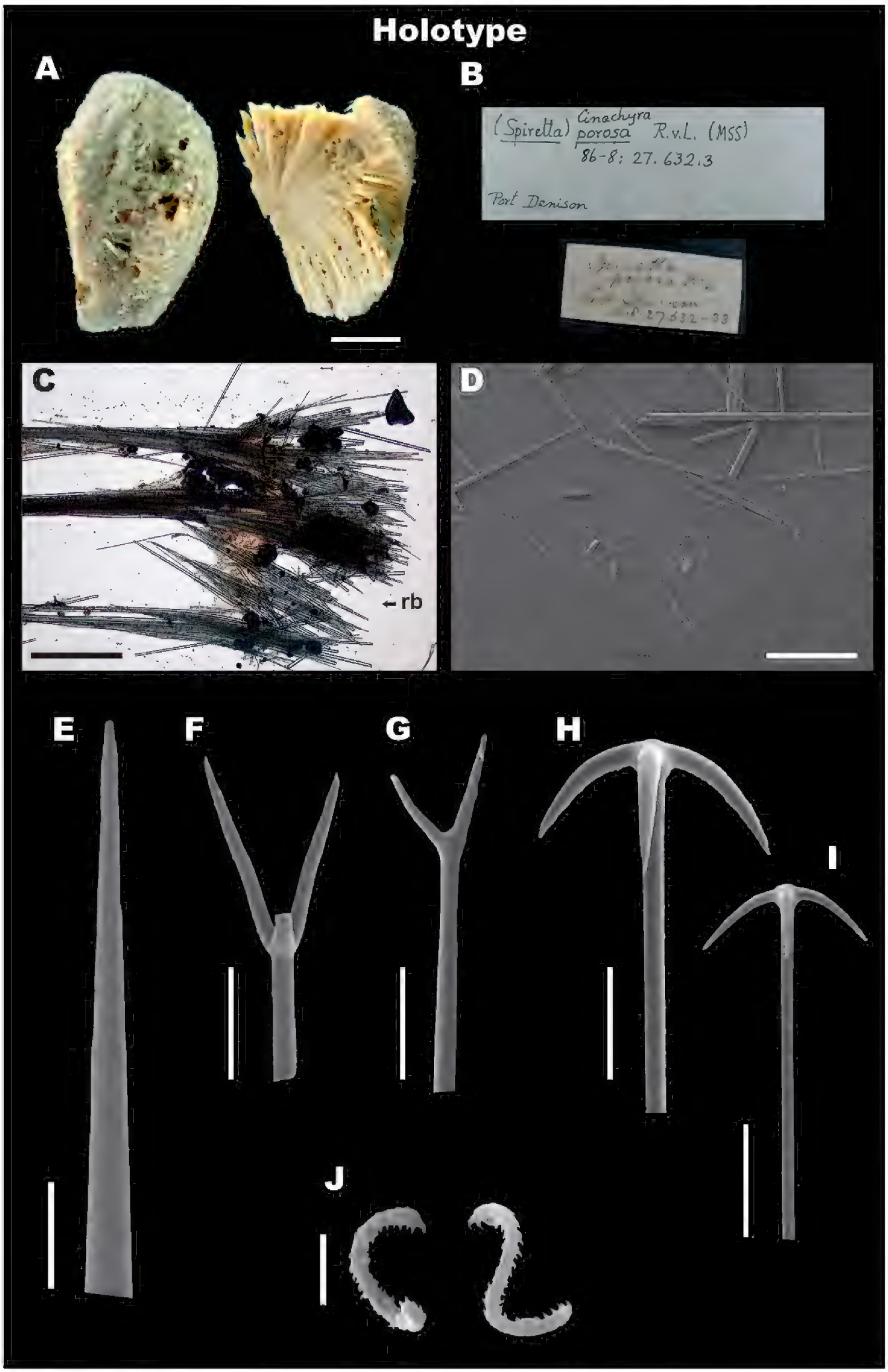


**Figure 9.** *Cinachyrella porosa*. Holotype NHMUK1886.8.29.632-633, Port Denison, Australia. **A** preserved material showing porocalices and internal structure **B** Labels of the type specimen **C** skeleton **D** electron micrograph showing oxea fragments and triaenes rhabds **E** oxea, end detail **F** protriaene **G** prodiaene **H, I** anatriaenes **J** sigmaspires. Scale bars: 1 cm (**A, C**); 500 µm (**D**); 50 µm (**E**); 40 µm (**F–I**); 5 µm (**J**).

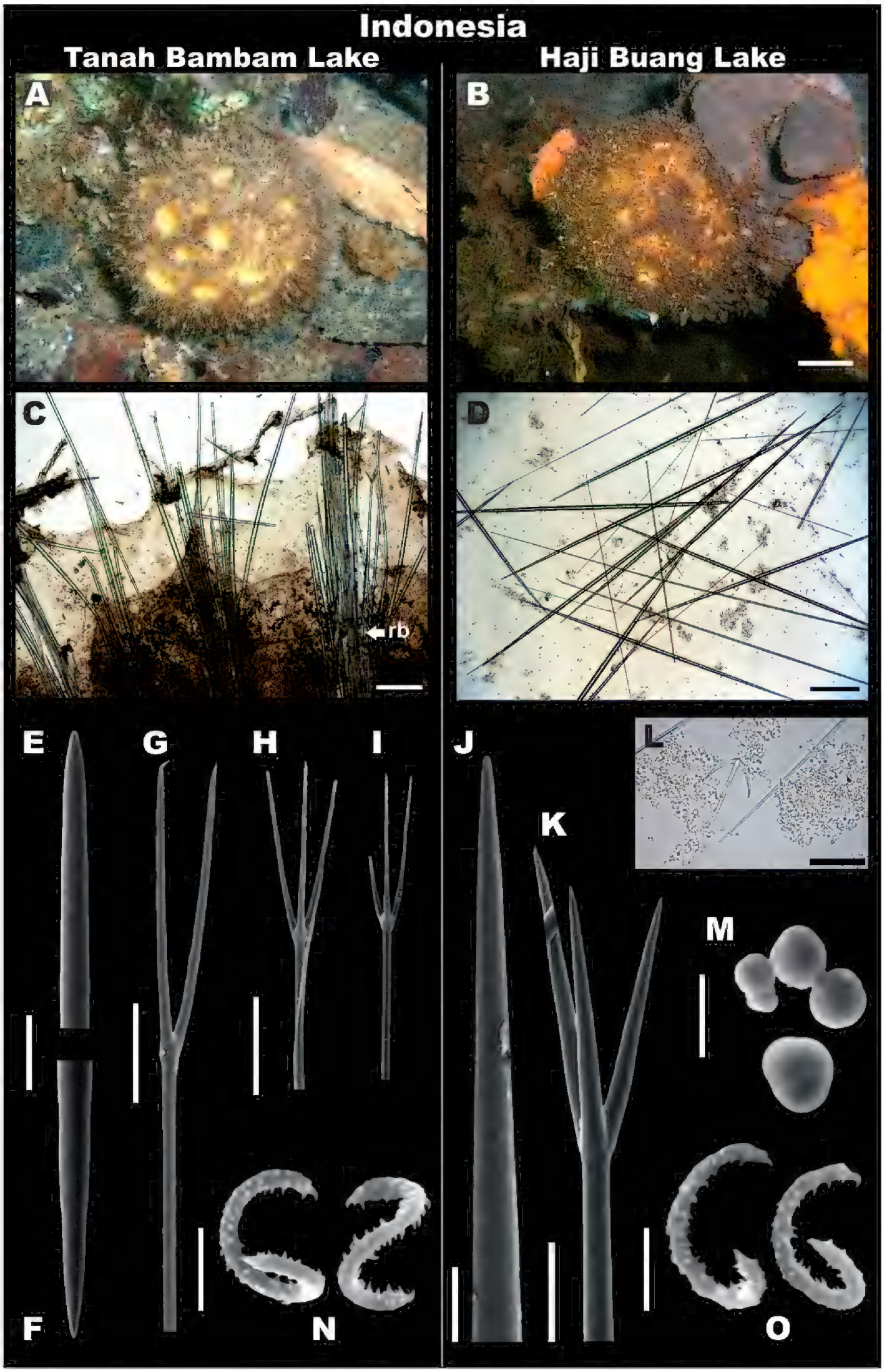


**Figure 10.** *Cinachyrella porosa* from Indonesia. A, C, E-I, N, RMNH.POR.11223, Tanah Bambam Lake. **B,D, J-M, O** RMNH.POR.11235, Haji Buang Lake **A-B** *In situ* photographs; **C** skeleton, showing radial bundles and triaenes **D** spicules in light microscope showing oxeas and triaenes rhabds **E, F** oxea, end details **G** prodiaene **H, I** protriaene **J** oxea, end detail **K** protriaene **L** anatriaene in light microscopy **M** spheres **N, O** sigmaspires. Scale bars: 500 µm (**C, D**); 20 µm (**E,F, J**); 40 µm (**G–I, K**); 100 µm (**L**); 5 µm (**M–O**).

Color generally yellow when alive (Figure 10A, B), which turns paler or even white-grey after preservation in ethanol (Figure 9A).

**Skeleton.** No cortex. Skeleton composed by bundles of oxeas and triaenes radiating from a central core (Figs 9C, 10C).

**Megascleres**. Measurements are shown in Table 6 for the holotype and Indonesian specimens. Holotype, oxeas 820–2553.2–3750 μm × 7.5–29.4–47.5 μm (Figure 9C-E); few anatriaenes (Figure 9H, I), with rhabd always broken 2.5–7.3–15 μm, cladi thin, with obtuse angles 50–67.6–100 μm × 30–42–60 μm × 2.5–5.6–7.5 μm; protriaenes less abundant (Figure 9F), with rhabd always broken up to 5800 μm × 5–7.3–12.5, probably tapering to dimensions < 1 μm, with thin and long cladi (25–44.4–65μm × 35–73–110μm × 5–5.1–7.5 μm); abundant prodiaenes with similar dimensions as protriaenes (Figure 9G).

**Microscleres.** No microxeas. Sigmaspires 5–8.6–12.5 μm in the holotype (Figure 9J) and 5–8.4–12.5 in the Indonesian specimens (Figure 10N, O), C-S shape; in some Indonesian specimens, silica spheres ranging from 3–7 μm in diameter can be present (Figure 10M).

**Ecology.** Occurs in reefs, mangroves, and marine lakes. Predominantly in shallow areas. Notably, a large population inhabit the marine lake of Tanah Bambam, where *C. porosa* was the dominant representative of moon sponges. This species produces 1–2 mm sized buds (Figure 8) and buds extensively in marine lakes habitats.

**Distribution.** According to the material examined in this revision, we observed that this species is widely distributed in the Indo-Pacific, from the Chagos archipelago, Sri Lanka, Australia, and Tonga Islands. In Indonesia, *C. porosa* has been collected in East Kalimantan, Java, Ternate, and West Papua.

**Remarks.** *Cinachyrella porosa* is distinguished from *C. australiensis* by the absence of acanthose microxea and smaller size of sigmaspires. The first species described with these two diagnostic characteristics was *Spiretta porosa* Lendenfeld, 1888, subsequently transferred to the genus *Tetilla* (Lendenfeld 1903) and included as a junior synonym of *C. australiensis* in both, Burton (1934) and WPD (2018). The detailed examination of the holotype of *C. porosa* suggests that this species should therefore be resurrected. Based on the careful examination of the holotypes of *C. albabidens* (Lendenfeld, 1907) and *C. albaobtusa* (Lendenfeld, 1907), and the descriptions and plates of *C. malaccensis* (Sollas, 1902) and *C. clavigera* (Hentschel, 1912), we coincide with the *porosa*-group recognized by Burton (1934). However, we disagree with the statement that intermediate forms can be found within the wide range of variation of *C. australiensis*, and therefore we consider *C. porosa* as a valid species clearly differentiated from *C. australiensis*. Lendenfeld (1907) recognized the difficulties to separate the three species of the alba-group, and his decision to discriminate them as different species was based on distant localities and slight differences on the abundance of triaenes. After the morphological analysis of the *C. albatridens* holotype, we consider that this species could also be a junior synonym of *C. porosa* because neither microxea nor other characters to separate this species were found. Although Burton (1934) did not consider *C. anomala* (Dendy, 1905) within the *porosa*-group, we suggest that a similar decision could be

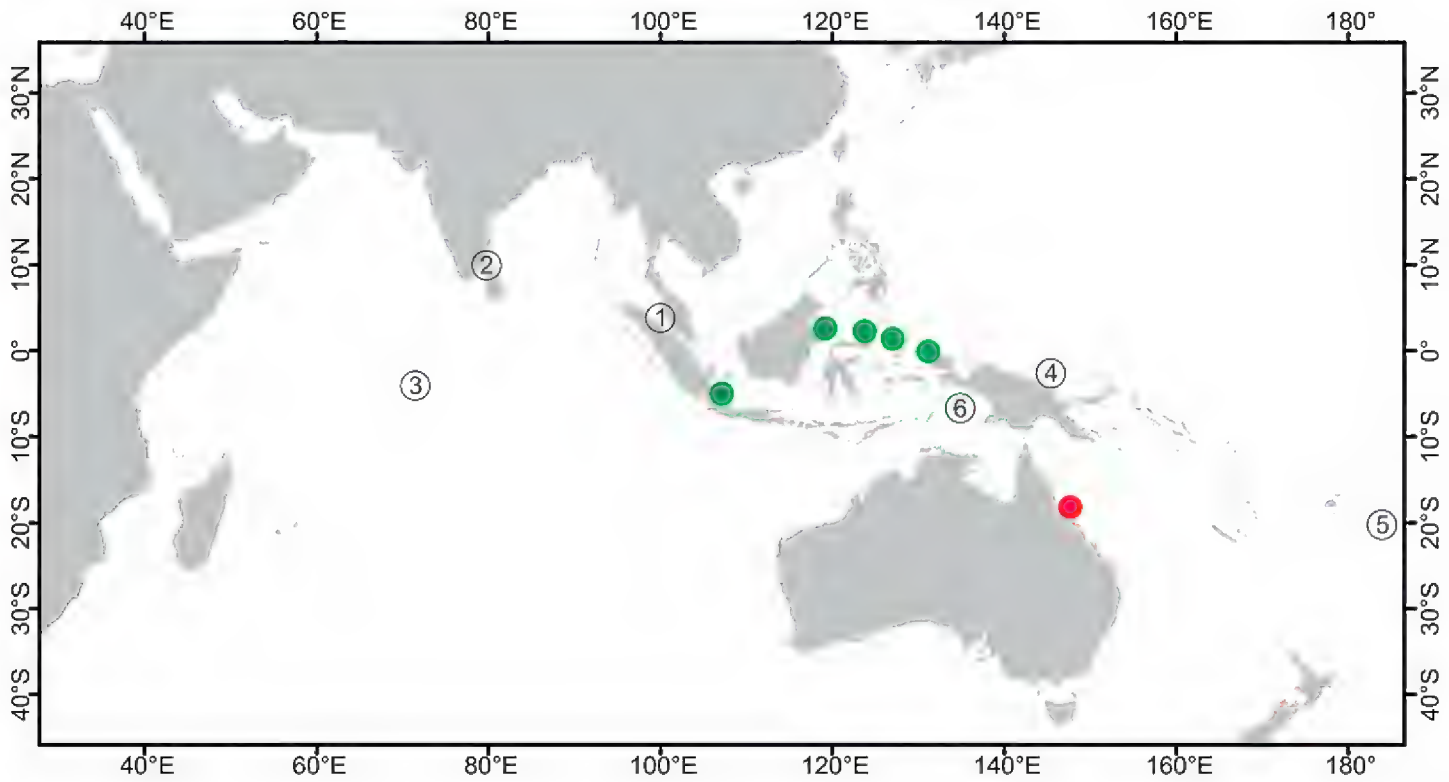


**Figure 11.** Distribution of *Cinachyrella porosa*. Red dot: type locality, *Spiretta porosa* Lendenfeld, 1888, Port Denison, Queensland, Australia. Green dots: Indonesian localities where the species was collected recently. Circled numbers: type localities of synonymized species **1** *Cinachyra malaccensis* Sollas, 1902, Malacca Strait, Malaysia **2** *Tetilla anomala* Dendy, 1905, Chilaw, Sri Lanka **3** *Cinachyra albatridens* Lendenfeld, 1907, Diego Garcia, Chagos Archipelago **4** *Cinachyra albaobtusa* Lendenfeld, 1907, Anachoreten (=Keniet) Islands, Papua New Guinea **5** *Cinachyra albabidens* Lendenfeld, 1907, Tonga Islands **6** *Tethya clavigera* Hentschel, 1912, Aru Island, Indonesia.

made based on our observations of the type specimen. Some of the Indonesian specimens have silica micro-spherules. Similar spherules have been described for species *C. anomala* and *C. hirsuta* (Dendy, 1905), as well as *Tetilla cinachyroides* (Hentschel 1911). Because *C. hirsuta* and *T. cinachyroides* contain acanthose microxea, they are synonimized with *C. australiensis*. The nature of these spherules has been discussed by Dendy (1905) and Lendenfeld (1907). Dendy (1905) suggests that the spherules are associated with mother cells, which probably would give origin to sigmaspires, or they can be considered as anomalous or incidental spicules. On the other hand, Lendenfeld (1907) estimated that spherules are the earlier stages of oxeas as described for *Tethya cranium* (see Lendenfeld 1907, plate 14 figs 11–15). Silica spherules are very variable within populations of the same species and among different genera in Tetillidae, suggesting that this character has no taxonomic value.

### *Cinachyrella paterifera* (Wilson, 1925)

Figs 12, 13

*Tetilla (Cinachyrella) paterifera* Wilson, 1925: 375; plate 39, figs 6, 8; plate 48, fig. 4 (type seen).

**Material examined.** Holotype USNM21314, South of Tumindao Reef, Tibutu Island, Sibutu Group, Sulu Archipelago, Philippines, 18 m, 27 Feb 1908. **INDONESIA**. East Kalimantan, *Berau reef,* RMNH.POR.11207; RMNH.POR.11208; RMNH.POR.11209; RMNH.POR.11211. West Papua, *Wallace Lake,* RMNH.POR.11212, RMNH.POR.11213, RMNH.POR.11214; *Outside Wallace Lake,* RMNH.POR.11215; *Gam Island,* RMNH.POR.11216, RMNH.POR.11217, RMNH.POR.11218, RMNH.POR.11219, RMNH.POR.11220; *Ctenophore Lake,* RMNH.POR.11221.

**Description. External morphology**. Globular sponges, size from 5 to 7 cm in diameter attached to the substrate by a large peduncle/shaft 3 × 2.5 cm (Figure 12 A, B). Surface smooth to hispid due to the projecting spicules, covered by porocalices. Porocalices are bowl or pocket-shape, with rounded apertures, up to 5 × 7 mm and 2–4 mm deep; a central cloaca is located on the top, 15 × 12 mm in diameter and 10 mm deep. Color bright pink when alive, which turns slightly paler in ethanol. Skeleton composed by bundles of oxeas and triaenes radiating from a central core. No cortex.

**Megascleres.** The holotype and Indonesian measurements are shown in Table 6. Holotype, oxeas 1400–3011.5–4750 µm × 10–34.5–62.5 µm (Figure 12D, I); few anatriaenes (Figure 12L), with a thick, small, poorly developed cladi, 17.5–24.2–30 µm × 2–6.5–10 µm × 5–5.8–7.5 µm, rhabd slightly thicker in the middle 15–25 µm, and tapering to dimensions of < 1 µm.; two different types of protriaenes, first one rare, with thick and small cladi (Figure 12K), 30–32.5–35 µm × 22.5–31.3–40 µm × 7.5–7.5–7.5 µm, rhabd usually broken, up to 5000 × 10 µm, thicker in the middle 40 µm, and tapering to dimensions of < 1 µm, the second type smaller, very abundant around porocalices, with small cladi in acute angle (fork-shape), 7.5–12.5–17.5 µm × 12–15.5–20 µm × 2.5–2.5–2.5 µm, rhabd up to 820 × 2.5 µm; strongyles are common, although only broken spicules observed in the holotype (Figure 12J), Indonesian specimens are 1800–2545.8–3700 µm × 35–42.7–62.5 µm (Figure 12F); no calthrop-like triaenes.

**Microscleres.** No microxeas; sigmaspires 10–13.2–17.5 µm in the holotype (Figure 12N) and 10–14.8–20 µm in Indonesian material (Figure 12M); C-S shape.

**Ecology.** The species occurs mainly in reefs, and it is rare in marine lakes and mangroves. It usually inhabits sand bottoms, in which the penduncle serves as a support structure.

**Distribution.** Indonesia, including East Kalimantan and West Papua. It is also known from Sibutu Island in Philippines (Wilson 1925). Although it is found in a variety of habitats, *C. paterifera* is the least common species of *Cinachyrella* from Indonesia.

**Remarks.** *Cinachyrella paterifera* has a characteristic elongated peduncle, it is pink to violet colored, and it contains abnormal anatriaenes. Interestingly, Wilson (1925) described rare microxeas (250 × 2 µm) in one specimen of the type series, whilst they were very abundant in the other two types. After a detailed examination of the type specimen USNM 21314 and preparations from different parts of the individual sponge, no microxeas were observed, suggesting that this character is not diagnostic of the species. Although *C. tenuiviolacea* (Pulitzer-Finali 1982) from the Great Barrier Reef resembles *C. paterifera* in the distinctive pink to violet color and presence

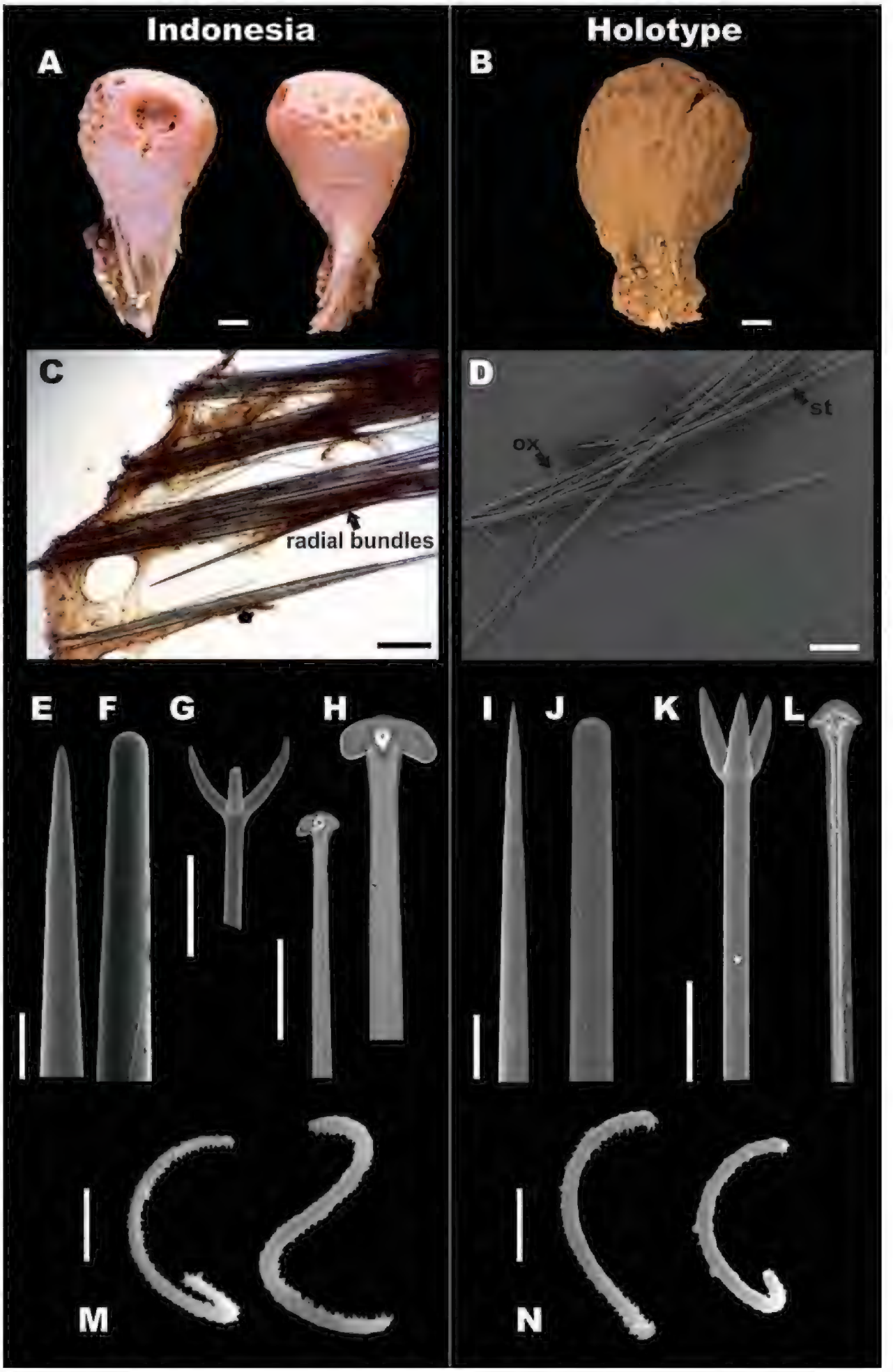


**Figure 12.** *Cinachyrella paterifera*. **A, C, E-H, M** RMNH.POR.11207, Berau Reef, Indonesia (left side). **B, D, I-L, N** holotype USNM 21314, Timundao Reef, Sulu Archipelago, Philippines (right side) **A** specimen recently collected showing typical pink color, porocalices and stalk **B** Holotype, showing porocalices and stalk **C** skeleton showing radial bundles **D** spicules showing oxeas (ox) and strongyle (st), (scale bar 500 µm); **E** oxea, end detail **F** strongyle, end detail **G** protriaene **H** anatriaenes with short or abnormal cladus **I** oxea, end detail **J** strongyle, end detail **K** protriaenes **L** anatriaene with short or abnormal cladus **M, N** sigmaspires. Scale bars: 1 cm (**A, B**); 500 µm (**C, D**); 40 µm (**E–L**); 5 µm (**M, N**)

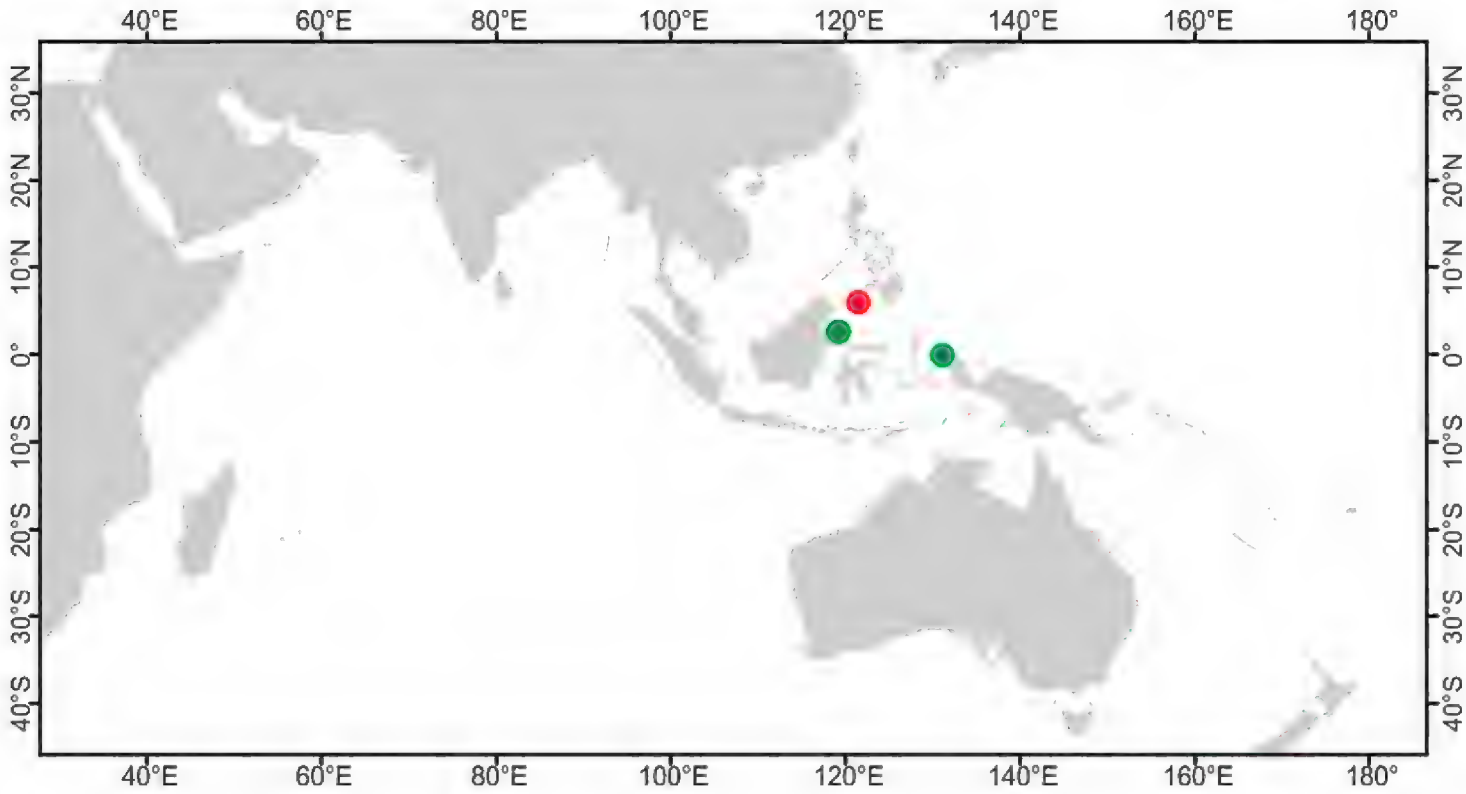


**Figure 13.** Distribution of *Cinachyrella paterifera*. Red dot: type locality, *Tetilla (Cinachyrella) paterifera* Wilson, 1925, Sibutu Island, Philippines. Green dots: Indonesian localities where the species was collected recently.

of abnormal anatriaenes, it remains to be investigated if these two species could be synonymized. We could not access type material from *C. tenuiviolacea*, and from the bad conditions of preservation noted by Pulitzer-Finali (1982) in his type specimen, it is not possible to determine whether the specimen has or does not have the peduncle characteristic of *C. paterifera*. The large numbers of hair-like protri- and prodiaenes around the porocalices of *C. paterifera*, resemble those described for *C. vaccinata* (Dendy, 1905), yet the *C. vaccinata* type contains acanthose microxea characteristic of *C. australiensis*. *Cinachyrella paterifera* share with *C. porosa* the absence of microxea, but they differ by the larger sigmaspires and abnormal protriaenes of *C. paterifera*. Indonesian specimens vary within the morphological range of the species. Specimens of this species belong to the same phylogenetic clade supporting its monophyly (Szitenberg et al. 2013; Schuster et al. 2017).

## Identification key for Indonesian *Paratetilla* and *Cinachyrella* species

1 Porocalices present; calthrops ..... **2**

– Porocalices present; no calthrops, all triaenes –if present– are long-shafted.... ..... **4**

2 Trichodragmata present ..... ***Paratetilla corrugata***

– Trichodragmata not present ..... **3**

3 High numbers of porocalices, small size (up to 5 mm), brown color ..... ..... ***Paratetilla bacca***

– Few porocalices, large size (7–15 mm), orange color, fleshy consistency..... ..... ***Paratetilla arcifera***

4 Microxea present ..... **5**
– Microxea not present ..... **6**
5 Acanthose microxea present (115–270 µm); sigmaspires 10–20 µm ..... ***Cinachyrella australiensis***
– Smooth microxea ..... ***Cinachyrella schulzei*-group**
6 Small sigmaspires (5–10, few up to 12.5 µm), generally yellow color and ball-shape ..... ***Cinachyrella porosa***
– Large sigmaspires (10–20 µm), generally pink color, sometimes with peduncle to attach it to the substrate, pear-shape; protriaenes in two different classes; few anatriaenes with reduced and deformed cladi ..... ***Cinachyrella paterifera***

## Final remarks

Our results contribute to the understanding of the taxonomy and systematics of the Indo-Pacific tetillids. A review of the taxonomic history of the genus *Paratetilla* and the species *Cinachyrella australiensis*, showed some cases of misinterpreted synonyms, misidentifications and lack of detailed descriptions for some species. The concept of a single widespread species is refuted for *Paratetilla bacca* (Dendy 1922, Burton 1959) as well as for *Cinachyrella australiensis* (Burton 1934). A wide morphological variation within moon sponges was observed for specimens collected in Indonesia. Among our material, we recognize three *Paratetilla* and four *Cinachyrella* species occurring in Indonesia, inhabiting a variety of habitats such as marine lakes, coral reefs, and mangroves. We are resurrecting *P. arcifera* Wilson 1925 and *C. porosa* (Lendenfeld, 1888) as valid species. The majority of the holotypes were studied for the current study; the ones we did not review were either unavailable or the description of the text was clear and comprehensive.

The species of *Paratetilla* and *Cinachyrella* are clearly highly adaptable and widely distributed sponges. All species in the current study are distributed across Indonesia. It is remarkable that they are all sympatric, some species occuring together in the same marine lake. We have reviewed specimens from East Kalimantan, North Sulawesi, and West Papua. It is highly likely that there are more species in Indonesia in regions that have not been sampled as extensively. Further investigations into *Paratetilla* and *Cinachyrella* from the Molluccas, Nusa Tenggara, South Kalimantan, Eastern Papua, and also the virtually unexplored deep sea of Indonesia, will likely lead to the discovery of more species within these genera. Most species occur in all studied habitats (marine lakes, mangroves, and reefs) with a high degree of tolerance for high temperature and sedimentation, as has been observed in other families of sponges (Schönberg 2015). The exceptions to this high tolerance were *P. arcifera* and *C. paterifera,* which were only seen in reefs with little sedimentation or sediment resuspension. High budding was observed in specimens of *Cinachyrella australiensis* and *C. porosa* residing in marine lakes, while no budding was observed in the same species in the reefs. Singh and Thakur

(2015) revealed temperature as the most prominent factor regulating the intensity of budding in *Cinachyrella* cf. *cavernosa*.

Previous molecular phylogenetic studies indicate that *P. bacca, P. arcifera, C. porosa,* and *C. paterifera* are distinct monophyletic species, while *Cinachyrella australiensis* may consist of a species complex with morphologically cryptic species (Schuster et al. 2017). In the specimens that we identify as *C. australiensis* we do not find any consistent differences in spiculation to validate distinct species, in spite of the different haplotypes that are found within our specimens. Carella et al. (2016) also found that several well-supported subgroups within the *Cinachyrella* clade might correspond to subgenera. We were not able to distinguish multiple species with our set of *C. australiensis* specimens using standard morphological characters. Among the reviewed literature, we also observed that there is a tendency among people making inventories of reef species to name any yellow or yellow-orange tetillid ball *C. australiensis*. It is clear that the genus *Cinachyrella* and in particular the species *C. australiensis* require further analysis using either other molecular markers or morphological characters that go beyond the aims of the current study. We hope that our detailed study, images, and key will ensure that species from *Paratetilla and Cinachyrella* will be identified correctly based on morphological characters. It is important to understand the distinction between species, as there is a growing interest in natural products and other biobased studies from tetillids (e.g. Cleary et al. 2013, Mokhlesi et al. 2017, Zhang et al. 2017). We expect that the current study can provide a solid basis for subsequent species descriptions of Indo-Pacific species of the genera *Cinachyrella* and *Paratetilla.*

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## Supplementary material 1

**Table S1. Full collection details of each sample**

Authors: Nadiezhda Santodomingo, Leontine E. Becking

Data type: species data

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Link: https://doi.org/10.3897/zookeys.791.27546.suppl1

## Supplementary material 2

**Figure S1. Type material of *Tethya merguiensis***

Authors: Nadiezhda Santodomingo, Leontine E. Becking

Data type: multimedia

Explanation note: NHMUK 1894.11.16.17, Mergui Archipelago, Myanmar. **A** two slide preparations of the type specimen **B** skeleton, showing anatriaenes and oxeas **C** oxea, anatriaene, and protriaene **D** thin microxeas and sigmaspires **E** sigmaspires. Scale bars: 100 μm (**B, D**); 50 μm (**C**); 20 μm (**E**).

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